

Ostrich (*Struthio camelus*) chick survival to 6 months post hatch: Estimation of environmental and genetic parameters and the effect of imprinting, foster parenting and deliberate care

by

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Summary

The South African Ostrich industry was established more than 100 years ago. Despite appreciable fluctuations and modifications in demand, the industry perseveres, with meat and leather as the current primary driving force. Low and variable early chick survival is globally considered as a major constraint in the industry. In spite of obvious welfare and production implications, research findings concerning ostrich chick survival are scant. Four studies involving chick survival to 24 weeks post hatch were thus performed.

South African Black ostrich (*Struthio camelus var. domesticus*) data obtained from a commercial pair-bred ostrich flock maintained at the Oudtshoorn Experimental Farm, South Africa comprising 10418 records were utilized to run a series of single- and multiple-trait binomial analyses using either linear models (ASREML) or threshold models (Monte Carlo Markov Chain methods, employing Gibbs sampling software) respectively. Suitable fixed and random effect models together with variance and (co)variance components were derived from these analyses. Ostrich chick survival to 24 weeks post hatch was low (28%) with a large environmental component. Pre-incubation storage time only affected 0 to 3 week survival, while incubator had a significant effect on cumulative survival traits to 24 weeks as well as on 13 to 24 week survival. Female chicks outperformed males at 0 to 12 weeks, 0 to 24 weeks, 4 to 12 weeks and 13 to 24 weeks with regard to survival. Hen age was significant for all traits except survival during the first week as well as for survival from 13 to 24 weeks post hatch. All analyses exhibited comparable low heritability estimates for all survival traits except for 0 to 1 week survival and 13 to 24 week survival ($h^2 = 0.12$ and 0.10 ; $m^2 = 0.08$ and 0.07 respectively) which demonstrated higher additive genetic and maternal components when threshold models, using Gibbs sampling algorithms, were employed. Neither moisture loss nor day of external pipping exhibited notable additive genetic correlations with any of the estimated survival traits. Day-old chick weight demonstrated a low correlation with early chick survival ($r_g = 0.24 \pm 0.19$) with heavier chicks tending to have a higher survival probability. The effects of rearing method on early chick survival and growth were also investigated. Comparisons between chicks reared and fostered by adult ostriches in a semi-extensive environment and chicks imprinted onto humans under an intensive system and between regular human handling in an intensive rearing system and the standard farm protocol of an intensive rearing system were made. No difference in the early chick survival to 3 weeks post hatch of chicks reared by foster parents and those chicks imprinted onto humans was demonstrated. At later ages, those chicks reared by foster parents outperformed human imprinted chicks. Human imprinted chicks exposed to regular handling demonstrate an enhanced early

survival when compared to chicks exposed to conventional rearing protocol in intensive systems. The study is seen to provide guidance for further research on this topic.

Opsomming

Die Suid-Afrikaanse volstruisbedryf is meer as 100 jaar gelede gevestig. Die bedryf is volhoubaar, ten spyte van 'n fluktuierende aanvraag na volstruisprodukte. Vleis en leer is tans die produkte wat die meeste tot die inkomste van boere bydra. Lae en wisselende kuikenoorlewing is 'n belangrike knelpunt in die bedryf. Navorsingsuitsette rakende kuikenoorlewing is skaars, ten spyte van ooglopende welsyns- en produksie implikasies. Kuikenoorlewing tot en met 24 weke na uitbroei is dus in vier afsondelike studies ondersoek.

Data van 10418 kuikens uit 'n kommersiële broeipaargeteelde Suid-Afrikaanse Swart (*Struthio camelus* var. *domesticus*) kudde op die Oudtshoorn Navorsingsplaas, Suid-Afrika is gebruik om enkel- en meervoudige eienskappe met of liniêre modelle (ASREML) of drempelwaarde modelle (Monte Carlo Markov Ketting metodes, met Gibbs monsterring sagteware) te pas. Die metodes is gebruik om toepaslike vaste- en toevalseffekte modelle saam met (ko)variensie komponente te bekom. Kuikenoorlewing tot 24 weke na uitbroei was laag (28%), met 'n groot omgewingsbydraende komponent. Stoor van eiers voor pak het slegs kuikenoorlewing van 0 tot 3 weke beïnvloed, terwyl die broeikas wat gebruik is 'n betekenisvolle invloed op kuikenoorlewing tot 24 weke ouderdom, sowel as op -oorlewing van 13 tot 24 weke gehad het. Wyfiekuikens het beter oorleef as mannetjie kuikens vir oorlewing gemeet van 0 tot 12 weke, 0 tot 24 weke, 4 tot 12 weke en van 13 tot 24 weke. Broeiwyfie ouderdom het 'n betekenisvolle invloed op kuikenoorlewing in die eerste week na uitbroei en van 13 tot 24 weke na uitbroei, gehad. Kuikenoorlewing was relatief laag oorerflik, behalwe vir oorlewing van 0 tot 1 week en vir oorlewing van 13 tot 24 weke van ouderdom ($h^2 = 0.12$ en 0.10 ; $m^2 = 0.08$ en 0.07 onderskeidelik). Drempelwaarde modelle met Gibbs monsterring algoritmes het hoër additiewe en maternale variensie verhoudings in vergelyking met liniêre modelle aangedui. Genetiese korrelasies van vogverlies en die dag van uitwendige pik met kuikenoorlewing was oor die algemeen onbeduidend. Dagoudkuikengewig is laag gekorreleerd met vroeë kuikenoorlewing ($r_g = 0.24 \pm 0.19$), met swaarder kuikens wat oor die algemeen beter oorleef. Die gevolge van verskillende grootmaak metodes op vroeë kuikenoorlewing en -groei is ook ondersoek. Vergelykings tussen kuikens grootgemaak deur volwasse volstruise as pleegouers in 'n semi-intensiewe omgewing en kuikens grootgemaak deur mense onder 'n intensiewe stelsel en tussen kuikens grootgemaak deur gewone menslike hantering in 'n intensiewe grootmaak sisteem onder standard plaas protokol was bestudeer. Geen verskille was gevind in vroeë kuikenoorlewing tot 3 weke na uitbroei, van die kuikens grootgemaak deur volwasse volstruise en tussen die kuikens grootgemaak deur mense. By latere ouderdomme, het die kuikens wat grootgemaak was deur volwasse volstruise beter oorlewing getoon as die kuikens grootgemaak deur mense. Kuikens grootgemaak deur mense wat blootgestel was aan

gereelde hantering het verhoogde vroeë oorlewing getoon in vergelyking met kuikens grootgemaak deur konvensionele grootmaak protokol in intensiewe stelsels. Die studie kan dus beskou word om leiding te verskaf vir verdere navorsing oor hierdie onderwerp.

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Chapter 1

General Introduction

A member of the Ratite family, the ostrich is the largest living bird and indigenous to the semi-arid and desert areas of Africa (Dolensek & Bruning, 1978; Griner, 1983). The domestication of the ostrich for commercial purposes took place more than 100 years ago in South Africa, and despite several constraints the industry remains a uniquely South African operation with its characteristic feather, meat and leather products (Deurden, 1919; Smit, 1963; Black, 2001). Although evidently temperamental when compared to other conventional livestock industries, the South African ostrich production industry is an important contributor to the global ostrich industry (DAFF, 2010). The production of a substantial number of good quality chicks surviving to slaughter is a vital component of selection and management objectives (More, 1996; Cloete *et al.*, 2002; Cloete *et al.*, 2008a). Few scientific studies have, however been conducted to identify breeding and management practices that enhance survival and early adaptation to the predominantly artificial rearing environment (More, 1996; Cloete *et al.*, 2001). High levels of hatching failure (Mellett, 1993; Deeming, 1995b) combined with low and extremely variable chick survival rates (Bunter, 2002) are primary factors constraining overall cost in the ostrich industry. The importance of investigating environmental, genetic and managerial components that potentially may predispose chicks to disease or increase the incidence of disease should be considered (Bubier *et al.*, 1996; More, 1996; Navarro *et al.*, 1998; Black, 2001; Cloete *et al.*, 2001; Navarro & Martella, 2002; Glatz & Miao, 2008).

Clear breeding objectives and industry breeding structures are largely absent, and the potential of environmental and genetic factors affecting ostrich chick survival are essentially unknown (Cloete *et al.*, 2008a). The determination of environmental and genetic factors will aid in the formulation of adapted management and breeding objectives that can potentially enhance the survival of ostrich chicks (Cloete *et al.*, 2002; Brand *et al.*, 2008; Cloete *et al.*, 2008a). Correlations between incubation traits, live weight traits, and other production traits are available in the ostrich industry (Bunter & Cloete, 2004; Cloete *et al.*, 2008b; Brand *et al.*, 2008), but no such correlations or estimates regarding chick survival have been reported to date.

General aspects of chick management and husbandry hypothetically, have a considerable impact on chick survival, but the ideal rearing system conducive to enhanced survival and optimal welfare and production is yet to be established (Jensen *et al.*, 1992; Alldredge, 1993; Wade, 1995; Glatz &

Miao, 2008). There is potential for improving the rearing environment of ostriches as well as other bird species, by identifying and manipulating those human factors that are influential in commercial units (Reed *et al.*, 1993; Hemsworth *et al.*, 1994). The amount of stress experienced by captive animals may be reduced subsequent to improvements, aimed at promoting their natural behaviour, in their environments (Jones & Waddington, 1993; Reed *et al.*, 1993; Savaterra *et al.*, 1994; Newberry, 1995). This may also prove constructive for their subsequent welfare and productivity. Foster parenting by adult ostriches, human imprinting and general habituation to human contact are potential ways of achieving such improvements (Mills & Faure, 1990; Jones & Waddington, 1992; Hemsworth *et al.*, 1993; Reed *et al.*, 1993; Rushen *et al.*, 1999). To date, little research has however been done on the implications, potential and scope of such practices in ostriches farming (Madeiros, 1997; Janse van Vuuren, 2008).

More systematic studies of chick survival would assist the industry in the development of adapted breeding and husbandry systems that reduce stress imposed on chicks while enhancing the ability of ostrich chicks to cope with and resist the effects of stress. Chick survival and the consequent cost-efficient commercial production of high quality slaughter ostriches could thus be optimized (Verwoerd *et al.*, 1999).

Ostriches from the Oudsthoorn Research Farm, South Africa were used in this study to investigate components of early ostrich chick survival. Aspects that were studied included the evaluation of systematic effects that affect age-specific chick survival, as well as genetic parameters for age-specific chick survival. Genetic correlations of day-old chick weight with incubation traits like evaporative water loss and pipping time were derived simultaneously, using both linear and linear-threshold models. Two additional studies investigated the effects of human imprinting, foster parenting and traditional intensive rearing practices on ostrich chick survival and early live weight.

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Chapter 2

Literature Review

Introduction

Commercial ostrich production commenced in South Africa during the 1860's (Deurden, 1919), after the commercial hunting of ostriches for their feathers was banned in the Cape colony. Despite the fluctuating nature of the industry, South Africa remains the prime exporter of ostrich meat, generating approximately R1.2 billion annually through foreign exchange (Black, 2001; DAFF, 2011). Low hatchability and poor chick survival are two primary factors constraining the industry (Cloete *et al.*, 2001; Glatz & Miao, 2008). The production of good quality chicks surviving to slaughter is essential for cost-efficient commercial production, as well as sufficient numbers of breeder replacement birds for selection in breeding programmes (More, 1996; Cloete *et al.*, 2002a). However, few studies have investigated aspects of ostrich chick survival (Cloete *et al.*, 2001; Wang *et al.*, 2011).

This chapter therefore provides an overview of the ostrich industry together with current knowledge of the effect of breeding and management, as well as chick rearing practices and behaviour, on chick survival.

The Ostrich

The largest of all extant bird species, ostriches are characterized by the absence of a breastbone, and therefore an inability to fly (Smit, 1963). Classified together with cassowaries, rheas, emus and kiwis, ostriches fall in the order of *Ratitae*, family *Struthionidae* and genus *Struthio* (Sclater, 1906; Sibley & Ahliquiste, 1990; Cooper *et al.*, 2009). Five ostrich subspecies that differ to some extent pertaining to egg size, eggshell texture and porosity, skin colour, body size, baldness and neck feathers, have been identified in Africa (Deurden, 1919; Madeiros, 1995; Jarvis, 1998; Cooper *et al.*, 2009). The subspecies *S. camelus syriacus* is extinct (Deurden, 1919). The *S. camelus camelus* and *S. camelus massaicus* comprise the Red Neck subspecies, while the *S. camelus molybdophanes* and *S. camelus australis* encompass the Blue neck subspecies (Madeiros, 1995; Jarvis, 1998). The *S. camelus* var. *domesticus*, a composite breed from crosses between *S. camelus camelus* and *S. camelus* var. *australis*, was developed in South Africa over years of breeding for an improved feather quality (Maderios, 1995; Petite & Davis, 1999). *S.c.* var.

domesticus are currently being farmed with for commercial purposes in South Africa, and the rest of the world (Swart, 1987; Jarvis, 1998; Engelbrecht *et al.*, 2008). The *S. camelus* var. *domesticus*, identified as the South African Black, is the most preferred breed in the South African ostrich production industry (Maderios, 1995; Petite & Davis, 1999). The South African Black ostrich weighs on average less, has a higher reproductive efficiency as well as a higher chick survival rate, when compared to the other above mentioned subspecies (Maderios, 1995; Jarvis, 1996; Lambrechts, 2004; Essa & Cloete, 2006). Selection for birds producing the best marketable plumage was however coupled with traits like growth rate and egg production being neglected as potential production parameters (Swart *et al.*, 1987, Maderios, 1995; Petite & Davis, 1999).

The Ostrich Industry

During the mid-1860's the domestication of ostriches in South Africa was primarily driven by the production and utilization of their feathers (Smit, 1963; Black, 2001; Cooper, 2001). During 1863, the export of ostrich feathers, primarily sourced from the Oudsthoorn area, was graded fourth in terms of importance of South African export merchandise (Smit, 1963). The industry however, collapsed in 1913 due to the impracticality of ostrich feather fashion in open automobiles as well as the onset of World War I (Deurden, 1919; Petite & Davis, 1999; Black, 2001). Between 1913 and 1930, the number of domesticated ostriches declined from a million to approximately thirty thousand, only partly recovering again in 1945 (Smit, 1964; Black, 2001). The re-emergence of ostrich farming after the Second World War took place in South Africa, and eventually commenced in several other countries (Black, 2001). The first local ostrich abattoir was set up in 1965, shortly followed by the establishment of the Klein Karoo Co-operative Ltd tannery in 1970 (Van Zyl, 2001).

The relative contribution of ostrich products to the monetary yield (income generated from?) of slaughter ostriches comprises of 45% meat, 45% leather and 10% feathers (DAFF, 2011). As the primary international supplier of ostrich products, South Africa contributes 67% to the global trade in ostrich products (meat, leather and feathers) (DAFF, 2011). Since the 2001/2002 increase to 355 725 ostriches slaughtered in South Africa per annum, a number of outbreaks of Avian Influenza have led to a great decline in the number of birds being slaughtered, with 222 000 birds being slaughtered during 2008/2009 (DAFF, 2011). A trend towards a healthier lifestyle has led to an increased demand for South African ostrich meat. Although the production of ostrich meat decreased by 18.4% from 2000/01 to 2008/09, the local consumption thereof increased by 29.9% (DAFF, 2011). The increase in the local consumption ensured that the industry was not only reliant on international markets for meat exports.

The total gross value of the ostrich production industry from 1999 to 2010 amounted to R3 876 million. An outbreak of Avian Influenza in 2003/04 led to an export ban that lasted 15 months, resulting in a decline in the gross contribution of the ostrich industry to the revenue from agricultural products. Despite this, the contribution of the ostrich industry to the total value of agricultural production has gradually increased since 1999. The export of ostrich meat to the European Union was recently under suspension due to an outbreak of highly pathogenic Avian Influenza in the Western Cape Klein Karoo area (DAFF, 2011). Approximately 70% of national ostrich farming activities are concentrated in the Klein Karoo district, and the socio-economic impact such a suspension is quite severe (DAFF, 2011).

Importance of genetic evaluation and selection

Genetic evaluation of livestock and sustained improvement of production traits, defined by Petit & Davis (1999) as any characteristic that can be visually identified or measured, has become common place over recent decades (Banks 2005; Graser *et al.*, 2005). Increasingly considered to present the most consistent means of eliminating destructive traits and endorsing desirable traits in livestock species (Jones, 1996; Faure & Mills, 1998), annual genetic improvement is particularly impressive in the more intensive industries (i.e. poultry, dairy cattle and pigs). This generalization does however not apply to the ostrich industry (Cloete *et al.*, 2008a).

Much of the ostrich genetic selection programs have, until recently, extrapolated heritability estimates from other species, particularly poultry (Black, 2001). Ostriches and poultry however have distinctly different population structures, management and production systems (Bunter & Cloete, 2004; Cloete *et al.*, 2006a).

Scientifically based selection and breeding strategies specific to ostriches are necessary for the improvement of production in the ostrich industry as a whole (Swart & Lambrechts, 1998). A greater emphasis on genetic improvement of birds with enhanced production and reproductive traits is vital to comply with or supply in specific future market needs (Petite & Davis, 1999). Appreciable phenotypic variations evident in several prominent traits demonstrate the latent benefits of selective breeding programs if differences are indicative of genetic variation (Jones *et al.*, 2002). According to Black (2001) a 10 % increase in egg production and hatchability corresponded with a 31% increase in profit, while a 10% increase in chick mortality rates corresponded with a 35% reduction in profit. Obtaining genetic parameters for reproduction and performance traits of ostriches is complicated by several factors i.e. the population dynamics, pair-mating structures and the inclination of the industry towards flock mating (Cloete *et al.*, 1998;

2002a; Bunter & Graser, 2000; Bunter & Cloete, 2004). Evidence suggesting that ostriches are induced breeders, are territorial, and create pair bonds with their mates as well as the small flock size and the long productive life of ostriches also limit the turnover of breeding stock, reducing both the number of parents with progeny and generations with record representation (Bunter & Cloete, 2004). The recording of data suitable for genetic analysis is compromised by these complications (Bunter & Cloete, 2004; Petite & Davis, 1999; Cloete *et al.*, 2002a; 2008). Despite these barriers, accurate parameter estimates for various ostrich production traits have recently become available (Cloete *et al.*, 2008). Based on the current levels of performance of many ostrich farms internationally, there is significant potential for improvement of production traits and product quality, particularly in terms of the cost-effective management of large commercial operations (Black, 2001).

Important traits in ostrich breeding

The primary revenue for the ostrich industry is generated from slaughter production, with considerable emphasis being placed on meat and leather traits (Petit & Davis, 1999; Bunter & Graser, 2000; Cloete *et al.*, 2002b). There has been much debate regarding the ideal slaughter age of ostriches (Jarvis, 1996a; Henderson, 1996; Van Zyl, 1996a). In South Africa, ostriches were initially slaughtered at 14 months of age as this appeared to be when optimal skin and nodule size were attained (Jarvis, 1998). Feathers from slaughter birds were selectively harvested around 7 to 8 months of age, guaranteeing a mature feather yield with the best follicle (mature) development at slaughter (Angel, 1996). Increased attention to skin damage as an important economic factor influencing leather quality, as well as increasing feed costs, however, favoured slaughtering birds at a younger age (Cloete *et al.*, 1998). A recent study by Bhiya (2006) found birds slaughtered at an older age corresponded with a significant increase in feed consumption and slaughter weight, as well as with undesirable effects on the skin grade. Birds slaughtered at 10.5 months represented the highest income generating group, producing on average between 40.6-42.9 kg of meat, 140-143 dm² of skin and 1.55-1.65 kg of feathers (Bhiya, 2006). Ostrich skin or leather is classified as being exotic, and is primarily supplied by South Africa (Cooper, 2001).

A skin produced per slaughter bird can weigh between 1.0 and 1.5kg, and is valued according to the size of the skin, the number of detectable defects (or degree of skin defects), and the shape and size of the feather nodules (Hallam, 1992; Engelbrecht *et al.*, 2009). Of the leather traits, only the size of the skin (surface area) can be measured objectively by (Engelbrecht *et al.*, 2009). Other objective methods of determining leather quality are time-consuming (Cloete *et al.*, 2006b) while other methods currently in use in the industry (skin damage or nodule development) can be

considered subjective, and thus unreliable when management decisions need to be made (Van Schalkwyk, 2008). Slaughter weight, skin size and skin quality are, therefore important slaughter traits, directly affecting the economic value of the bird (Cloete *et al.*, 2008a; Engelbrecht *et al.*, 2009).

Of the growth and slaughter traits, only leather thickness exhibits low heritability ($h^2 = 0.06$). Genetic gains for all other growth and slaughter traits are supported by moderate to high heritability's, falling between 0.18 and 0.46 (Bunter *et al.*, 1999; Bunter & Cloete, 2004; Engelbrecht *et al.*, 2005; Engelbrecht *et al.*, 2007; Cloete *et al.*, 2008b). High and favourable genetic correlations between skin and live weight traits suggest indirect selection for leather traits is achievable (Engelbrecht *et al.*, 2005; 2007)

Reproductive success of ostriches does to a large extent determine the quantity of slaughter progeny produced, and therefore has a considerable effect on the profitability of commercial ostriches (Bunter *et al.*, 2001a; Cloete *et al.*, 2004). The sale of day old chicks also forms an important source of the revenue of ostrich chick producers (Cloete *et al.*, 2008a).

Marked by large variation and limited research, reproduction, egg and chick traits have formerly been disregarded in the planning of ostrich breeding programmes (Petite & Davis, 1999; Bunter *et al.*, 1999; 2001b; Bunter & Cloete, 2004; Lambrechts, 2004; Cloete *et al.*, 2005a; 2005b; Cloete *et al.*, 2008b; Brand *et al.*, 2009). High levels of phenotypic variation together with evident between breed discrepancies indicate potential reproduction gains through genetic selection (Cloete *et al.*, 2008b; Engelbrecht *et al.*, 2008; Davids, 2011).

Reproductive traits are grouped as either quantitative traits (i.e. traits like egg production, which encompass the magnitude of production) or qualitative traits (i.e. traits concerning the quality/grade of production such as egg weight) (Cloete *et al.*, 2008a). Quantitative ostrich production traits are characterized by considerable variation, with coefficients of variation often exceeding 50% (Cloete *et al.*, 2008b). Quantitative reproductive traits typically exhibit low to moderate levels of genetic variation ($h^2 = 0.10-0.30$; Bunter *et al.*, 2001a; Cloete *et al.*, 2004; 2005a). In contrast, qualitative reproduction traits commonly exhibit coefficients of variation of 10% or less (Bunter *et al.*, 2001a; Cloete *et al.*, 2004; 2005a; Brand *et al.*, 2008a). Heritability estimates are also much higher ranging between 0.44 and 0.72 for average egg weight, and 0.51 and 0.74 for average chick weight (Bunter *et al.*, 2001a; Cloete *et al.*, 2004; 2005a; Brand *et al.*, 2008a).

Based on this information, selection is expected to benefit both quantitative and qualitative reproduction traits (Bunter & Graser, 2000). Genetic correlations among reproduction traits were generally favourable or negligible, while reproduction was also not negatively associated with live weight (Cloete *et al.*, 2005a; Cloete *et al.*, 2006a; Bunter *et al.*, 2001b; Cloete *et al.*, 2004; Cloete *et al.*, 2008b). An environment promoting or enabling egg and chick production would therefore be conducive to improved egg and chick weights (Cloete *et al.*, 2008b). Directed selection for chick production led to additive genetic gains amounting to 2-3% per annum, which is on par with what is expected in other species (Cloete *et al.*, 2004; 2008b).

Reproduction traits together with growth and feed efficiency traits can be considered as being of utmost importance for selection purposes (Engelbrecht *et al.*, 2005). Unfavourable correlations have been reported to exist between growth and reproductive traits in poultry (Bunter, 2002). In ostriches, live weight, egg and chick production exhibit insignificant correlations that are very near to zero (Cloete *et al.*, 2008b). The potential unfavourable relationship found between hatchability and day old chick weight has been attributed to breeding birds being overweight rather than underlying unfavourable genetic correlations (Van Schalkwyk & Cloete, 1996; Bunter, 2002; Cloete *et al.*, 2006a). Selection for reproduction and growth may therefore be simultaneously achieved (Cloete *et al.*, 1998; Cloete *et al.*, 2002b; Lambrechts, 2004), and therefore sustainable genetic improvement in the reproduction, growth and slaughter traits of ostriches is attainable (Cloete *et al.*, 2008b).

A critical trait that is currently not estimated and part of the present genetic parameter estimates for performance and reproductive traits of ostriches, is the absence of variance and covariance components for ostrich chick survival (Bunter & Graser, 2000; Cloete *et al.*, 2008a). Previous studies on ratite species indicated that overall levels of chick survival are presently low with marked variation and pronounced effect on the economic viability of commercial operations (Navarro *et al.*, 1998; Bunter & Graser, 2000; Navarro & Martella, 2002). With industry revenue essentially generated by slaughter birds, the current high level of chick mortalities is negatively affecting cost-effective ostrich production (Bunter & Graser, 2000). A pivotal challenge is therefore, the establishment of farming practices that synchronize genotype and environment, optimizing survival and subsequent production while improving the general welfare of ostriches (Glatz & Miao, 2008; Jensen *et al.*, 2008).

Ostrich chick survival

During the first couple of weeks of life, ostrich chicks are predisposed to various disorders, infections, diseases and stressors all of which can result in high mortalities that can range from 10 to 50%, within the first 3 months after hatch (Allwright 1996; Deeming, 1996; More, 1996; Verwoerd *et al.*, 1997; Bonato, 2009). According to a study done in Kenya in the 1979, Hurxthal reported that only 5 to 10% of chicks that hatch survive beyond the first year. Not much progress has been made in terms of improving chick survival. Cloete *et al.* (2001) concluded from their study that chick losses were high with only 20% of chicks that hatch survive beyond 90 days of age in an intensive domestic chick rearing system. In a study done by More (1996) chick survival was found to differ between farms. Some farms exhibited superior survival during the first month post hatch with high mortalities thereafter while other farms demonstrated low survival of chicks younger than a month with improved survival thereafter. According to Verwoerd *et al.* (1999) however, survival should be higher than 90% at 14 days of age for good quality chicks, and 95% between 3 and 12 months.

According to Uhart *et al.* (2006), impaired chick survival is largely the result of the removal of the birds from their natural wild habitat, and then introduced to intensive and semi-intensive farming conditions. General aspects of chick management and husbandry greatly influence chick survival, although the ideal conditions optimal for survival have yet to be established (Jensen *et al.*, 1992; Alldredge, 1993; Wade, 1995; More, 1996; Glatz & Maio, 2008). Parental conditions, incubation and hatching have a direct effect on the rearing of ostrich chicks, and optimal management thereof is essential to guarantee optimal survival and performance of young chicks to slaughter age (Verwoerd *et al.*, 1999; Black, 2001).

Artificial incubation

In an artificial incubation system, eggs are collected from the nest on a daily basis, thus preventing natural incubation by the parents. Differences of opinions exist regarding the best time for egg collection. According to Van Schalkwyk, (1998) eggs collected in the evening have a lower embryonic mortality than eggs collected in the morning. In turkey, a longer nest holding time enhanced the very early growth of the embryo (Fasenko *et al.*, 1994). There may be potential advantages of delaying egg collection from the nests as ostriches only begin incubation once all the eggs in the clutch have been laid (Deeming, 1996; Van Schalkwyk, 1998). Delayed egg collection does however expose the eggs to microbial contamination which corresponds with reduced embryonic survival (Deeming, 1996; Van Schalkwyk *et al.*, 1999b). Van Schalkwyk *et al.*

(1999) demonstrated delayed egg collection to have a slight, but insignificant impact on embryonic mortality.

Breeding ostriches may be maintained as adult breeder pairs or in ostrich breeder flocks (Deeming, 1997). In the latter, all the females lay their eggs in a single communal nest. In artificial management systems, eggs are collected daily from the nests and may be stored for a couple of days or placed directly in artificial incubators. The storage of eggs allow for eggs to be set in batches, allowing for hatcheries, to allow for chicks to be hatched in batches (Deeming, 1997; Ar & Gefen, 1998). The temperature at which eggs is stored may vary from 17 °C in temperature controlled rooms to more than 30°C on farms lacking such facilities (Van Schalkwyk *et al.*, 1999). Ideally, however, ratite eggs should be stored in temperatures between 25 and 27°C for a time period of 7 days or less and a relative humidity of 75% (Stern, 1991; Van Schalkwyk *et al.*, 1999; Brand *et al.*, 2007). Once storage time exceeds 7 days, embryonic abnormalities and mortalities increase, having to effect a prolonged incubation period and a decline in chick hatchability (Wilson *et al.*, 1997; Decuypere & Bruggeman, 2007). Studies in poultry demonstrated that the orientation of the egg during storage affect egg hatchability (Proudfoot & Hulan, 1983; Butler, 1991). Van Schalkwyk *et al.* (1999) however found the positioning of the egg during storage to have no effect on embryonic mortality.

Improved hatchability and subsequent survivability or viability of ostrich chicks are to a large extent determined by the optimal management of incubation conditions (Glatz & Miao, 2008). Eggs incubated in ideal conditions allow for the embryo to direct reserves to organ growth and development (Lourens *et al.*, 2005). A number of variable factors contribute toward the successful incubation of ostrich eggs and the subsequent hatching of good quality chicks (Lourens *et al.*, 2007; Decuypere & Bruggeman, 2007). Egg turning, egg orientation, humidity, temperature and respiratory gas exchange are physiological requirements of a developing embryo that can be managed in artificial incubators, and may have important implication for the subsequent hatchability of the eggs (Deeming, 1995a; Van Schalkwyk *et al.*, 1999).

Setting of eggs

Eycleshymer (1907) was one of the first to demonstrate the importance of egg turning in poultry, disclosing a 15% hatchability for eggs that had not been turned. Turning eggs during incubation stimulates the growth of the embryo while preventing the embryo from attaching to the inner shell membrane, and ensuring a uniform temperature around the egg, thereby ultimately enhancing the hatchability of the chick (Hallam 1992; Deeming 1993; Van Schalkwyk *et al.*, 2010). Cooper (2001)

reported that 85.7% hatchability for eggs laid, is attainable when eggs are positioned vertically and turned 8 times in a day. Van Schalkwyk *et al.* (2010) demonstrated that as the angle of vertically set eggs approaches 90° (rotated around the short axis), hatchability of eggs is increased. The negative effects of turning eggs through a smaller angle (60°) may, however, be negated by incubating eggs horizontally for a period of 2 weeks before eggs being set and incubated vertically (Van Schalkwyk *et al.*, 2010).

Humidity

The specific humidity maintained within the incubator should be calculated according to the average moisture loss for all those eggs produced by the flock within a season that are incubated artificially (Shane & Minter, 1996). Eggs lose moisture during incubation, the quantity of which largely determines the hatchability of fertile eggs set (Brand *et al.*, 2007). Attaining the ideal percentage moisture loss is however challenging, as it is affected by the condition within the incubator, the physical attributes of the eggshell as well as the internal dynamics of the developing embryo (Ar, 1991). A relative humidity maintained between 20 and 40% is considered as ideal for enhanced hatchability (Cooper, 2001).

Temperature

The temperature within the incubator affects the embryonic development, hatchability of the egg, as well as the post-hatch performance/growth of the chick (Romanoff, 1936; Van Schalkwyk *et al.*, 1999; Decuypere & Bruggeman, 2007). The conductance of heat between the incubator and the embryo, as well as the metabolic heat generated by the developing embryo influence the sensitivity of the embryo to the incubation temperature (French, 1997). Under natural incubation conditions, eggs are incubated at approximately 36°C (Swart *et al.*, 1987), while a temperature of between 35-37°C is considered to be ideal for artificial incubation (Deeming, 1993). Higher incubation temperatures correspond to elevated mortalities as well as an increased number of crippled and deformed chicks (Romanoff *et al.*, 1938). Young embryos incubated for a week at high temperatures (42.5°C) were characterized by having swollen kidneys and hearts, as well as heart failure (Leighton *et al.*, 1964). It has, however, been proposed that early embryos should be exposed to a slightly higher temperature than “optimum”, while older embryos should be exposed to slightly lower temperatures (Romanoff *et al.*, 1938; Tullet, 1990; Van Schalkwyk *et al.*, 1999). Tullet (1990) found that younger embryos responded to a 1°C increase in temperature with a 10% greater increase in metabolic rate than older embryos.

The second half of embryonic development is characterized by an increase in heat being generated by the embryo (Deeming, 1997). Overheating of the embryo during this time is therefore a risk, and can be avoided by changing the incubator temperature as the embryo develops (Ar, 1996). Despite the fact that the incubators are set at a specific relative humidity and temperature, the absolute conditions surrounding the eggshell may, however vary depending on the design of the incubator and the ambient conditions inherent to the specific incubator (Brand *et al.*, 2008a; Van Schalkwyk *et al.*, 1999a). Van Schalkwyk *et al.* (1999a) found forced draught wooden incubators to have higher temperatures (37°C) on the top tray together with those positions nearest the front and back of the incubator. They therefore proposed that because younger embryos are considered to be less vulnerable to excessive heat (Ar, 1996), they should be placed in those positions exposed to higher temperatures.

Ventilation

Air circulation is the movement of air within the incubator (Glatz & Maio, 2008). In order for the carbon dioxide released by the developing egg to be reduced and sufficient oxygen to be supplied, ventilation in the incubator is vital (Glatz & Miao, 2008; Van Schalkwyk *et al.*, 2002). Cooper (2001) suggested an airflow rate of about 45L/h/egg in the incubator. Every 1% reduction in oxygen relates to about a 5% decline in hatchability (Shane & Minter, 1996), and carbon dioxide levels of above 0.5% in the incubator give rise to an elevated number of embryonic deaths (Smith *et al.*, 1995). Van Schalkwyk *et al.* (2002) found the metabolic rate of the developing embryo to increase exponentially, attaining its peak between day 31 and 38 of incubation and then declining. Ventilation conditions within the incubator should therefore be adjusted according to the embryonic age and metabolic rate in order to accommodate the relative changes in gaseous exchange (Van Schalkwyk *et al.*, 2002).

Egg size and shell characteristics

The determination of the optimal conditions specific for individual eggs is complicated by the considerable variation in eggshell conductance and egg size demonstrated between eggs (Decuypere & Bruggeman, 2007). Under ideal conditions eggs that are of the same weight and size should be incubated together as this would optimize incubator conditions (Deeming & Ar, 1999).

The abovementioned incubation factors in conjunction with the physical properties of the egg/eggshell, internal embryonic factors together determine the extent of moisture loss by the egg

(Brand *et al.*, 2008b; Glatz & Miao, 2008; Deeming & Ar, 1999). The percentage of moisture lost by the egg during incubation is vital, as it determines the hydration status, hatchability, and subsequent day-old chick quality (Deeming & Ar, 1999; Adewumi *et al.*, 2008; Glatz & Miao, 2008). Deeming *et al.* (1993) suggested that a moisture loss of 13.4% is ideal for eggs incubated for 39 days. This would be similar to a 13.2% moisture loss that occurs under natural incubation conditions (Swart *et al.*, 1987). The moisture lost by the egg during incubation has a curvilinear relationship with embryonic mortality (Blood *et al.*, 1998), and excessive moisture loss to 35 days of incubation being linked to an increase in mortalities of 28-day old embryos (Cloete *et al.*, 2001). Blood *et al.* (1998) found moisture loss to be highly repeatable within a season. This was confirmed by Brand *et al.* (2009) who estimated a high heritability for percentage of water loss at both 21 days and 35 days of artificial incubation ($h^2 = 0.34$ and 0.27 , respectively).

Moisture loss and egg weight were found to be negatively correlated (Brand *et al.*, 2009). The relationship between egg weight and moisture loss is, however rather complex, with other factors such as eggshell porosity and structure also playing a role (Brand *et al.*, 2009). According to Fick's law of diffusion the "mass flow of a given fluid through a permeable barrier is directly proportional to the area available to diffusion and the concentration gradient of the fluid across the barrier (Cloete *et al.*, 2006c). The rate of flow is, on the other hand inversely proportional to the thickness of the barrier (Cloete *et al.*, 2006c). The structure and relative thickness of the eggshell are therefore important determinants of the amount of moisture lost by the egg during incubation (Paganelli, 1980). Marked variation in eggshell conductance is reported to exist between eggs (Cloete *et al.*, 2006c; Decuypere & Bruggeman, 2007).

In poultry, the age of the female or hen correlates positively with eggshell conductance, with that of older females producing eggs with an elevated eggshell conductance (Decuypere & Bruggeman, 2007). This is contradictory to findings of Cloete *et al.* (2006c), where shell traits were independent of the age of the female. The latter study, however, demonstrated shell thickness, pore area and pore area per unit shell thickness to be significantly affected by the month of lay. It was proposed that the properties of the shell may change relative to the climate, i.e. to ensure that a reasonably constant rate of water loss is maintained (Cloete *et al.*, 2006c). With a large variation in the eggshell conductance among eggs, the optimal conditions within the incubator vary (Decuypere & Bruggeman, 2007).

Hatching of ostrich eggs

On average, an ostrich chick will pip around 41.3 days after being set (Cloete *et al.*, 2001; Brand *et al.*, 2009). When the incubation period extends beyond 42 days, chicks are assisted to hatch (Brand *et al.*, 2009). Those chicks assisted have a reduced survival rate (25%), and exhibit extremely poor growth (Deeming & Ayres, 1994; Ipek & Sahan, 2004). Brand *et al.* (2009) found the time of pipping to be moderately heritable ($h^2 = 0.16$), which is lower than the corresponding estimate in female broiler breeders ($h^2 = 0.49$). Chicks that are stressed during incubation or that hatch under suboptimal conditions are expected to have a low survival probability, with less than 50% of eggs incubated hatching successfully (Cloete *et al.*, 1998; Deeming & Ar, 1999; Bunter, 2002; Lambrechts, 2004; Glatz & Miao, 2008).

Superior hatchability does not necessarily correlate with the hatching of good quality chicks, and cannot be considered a reliable indicator of excellent post-hatch development and viability (Tona *et al.*, 2004). However, according to Deeming (1996a), good quality day-old chicks tend to produce the best overall results. Day-old chick quality may be influenced by breeder age, egg storage, incubation environment and management practices (Tona *et al.*, 2004). There is however a lack of species specific information regarding the relationship between egg size, egg quality and chick development (Perrins, 1996).

Body weight reflects a combination of the condition and size of the ostrich chick (Cloete *et al.*, 2006a). Single-trait analysis of day old chick weight has produced high additive genetic ($h^2 = 0.34 \pm 0.07$) and maternal genetic estimates ($m^2 = 0.28 \pm 0.11$: Brand *et al.*, 2009). The strong positive genetic correlation between egg weight and chick weight, consistent across species, indicates that these traits are essentially controlled by the same or very similar set of genes (0.88-0.97: Wilson, 1991; Bunter & Cloete, 2004; Brand *et al.*, 2008a; Brand *et al.*, 2009).

Egg size has been reported to correlate with day old chick weight, chick size, growth rate and chick survival (Parsons 1970; Galbraith, 1988; Bolton, 1991; Perrins 1996). Early studies in precocial species demonstrated larger eggs to have an improved hatchability, and to allow for the hatching of heavier chicks with a large anatomical structure, superior post-hatch supplementation from the yolk, and a faster growth rate, all of which contribute to a better ability to survive (Parsons, 1970; Galbraith, 1988; Reid & Boersma, 1990; Bolton, 1991). Cloete *et al.* (2001) and Bonato (2009) found egg weight and subsequent day old chick weight to be an indicator of the survival of ostrich chicks to 1 month of age. Heavier chicks were found to have a greater ability to survive better (Cloete *et al.*, 2001; Bonato, 2009).

Hatchability and average chick weight were found to be not significantly genetically correlated (Cloete *et al.*, 2005a). No significant genetic correlation between individual egg or day-old chick weight, and later chick weights were found in a study by Bunter & Graser (2000). This suggests that selection for heavier chicks may not necessarily result in heavier slaughter birds. However, Cloete *et al.* (2001) proposed that chick survival may act as a form of natural selection for heavier birds at slaughter. The complexity of this relationship is yet to be investigated.

Parental quality attributes like age, breeding experience, or condition may also contribute to the size of the egg and offspring fitness (Reid & Boersma 1990; Bolton 1991). The relationship between egg size and the age of the hen appears to be quadratic. Herring gulls (*Larus argentus*) appear to lay the largest eggs at 8 years, after which a decline in the size of the eggs laid occurs (Bolton, 1991). Bunter & Cloete (2004) found the age of the hen in ostriches, accounts for 8% and 6% of the variation in egg and chick weights, respectively. Hens aged between 2 and 11 years produced heavier eggs, peaking with 6 year old hens and declining average egg and chick weights when the hen exceeds 11 years (Cloete *et al.*, 2006a).

In a recent study in poultry, younger breeders were found to produce smaller egg yolks with a different lipid profile to those of older breeders (Fasenko, 2008). Parental investment into egg composition may be a means of providing for precocial young during the critical post-hatch period (Galbraith, 1988). Containing antibodies, proteins, carbohydrates and lipids, the yolk sac is an energy dense nutrient source that is readily available to a newly hatched chick (Estaban *et al.*, 1991; Murakami *et al.*, 1992). The yolk sac contribute about 30-40% of a day old chick's weight, and rapidly declines in size as the chick grows as it is consumed, , supplying both nutrition and immunization (Verwoerd *et al.*, 1999). The exact rate at which the yolk sac is absorbed by a young ostrich chick is not yet established, with estimates varying from 7-10 days to 2-3 weeks (Smit, 1963; Jensen *et al.*, 1992; Verwoerd *et al.*, 1999). Yolk lipids provide the primary source of energy for the embryo and young chick, and the differences in yolk composition and size may be associated with hatchling health and survival (Estaban *et al.*, 1991; Bunter, 2002; Fasenko, 2008).

That which transpires during incubation and during the first couple of weeks post hatch may have a vital impact on the bird's health, growth and subsequent survival (Cooper, 2001; Fasenko *et al.*, 2009). An understanding of these processes will help in establishing a more conclusive impression of early chick survival.

Genetics

Survival is one of the primary fitness characteristics of a species (Istock, 1983). Variation in primary fitness characteristics creates the potential for natural selection to occur (Gebhardt-Henrich & Richner, 1998). Fisher's theorem of natural selection infers that those traits close to fitness traits demonstrate little or no heritable variation, as a result of robust directional selection on fitness, with those animals of lowered fitness not surviving to produce offspring (Istock, 1983).

In the process of domestication, populations of animals and their reproduction are largely controlled by man, and natural selection for enhanced fitness is subsequently disturbed (Price, 1997). Impaired ostrich chick survival may largely be the result of the removal of the birds from their natural wild habitat to intensive and semi-intensive farming conditions (Uhart *et al.*, 2006). The selection for ostriches more suited to the commercial rearing environment as well as the adaptation of rearing environments such that they are more conducive to the ostrich may have therefore have considerable implications.

Survival as a trait is however complex (Ducrocq & Solkner, 1994). A binomial trait, the distribution of survival is often skewed and statistical inferences are thus complicated (Kachman, 1999). The relationship between survival and time also poses a number of challenges, as data is thus censored with only the lower bound (alive period) of survival time being known (Ducrocq & Solkner, 1994; Kachman, 1999). The independent factors affecting survival may also vary with time (Ducrocq & Solkner, 1994). The accurate estimation of genetic components of survival is thus complicated.

To date only one preliminary study done by Wang *et al.*, (2011) has reported genetic parameters for chick survival in ostriches. Low heritability estimates were achieved, despite appreciable phenotypic variation. Low heritability estimates for traits however do not automatically specify a lack of genetic variation, and future gains can be expected in gradual progressions with the small flock sizes and low accuracy of selection (Bunter & Graser, 2000). Davids (2011) established a great degree of heterozygosity to be present within the ostrich population. Breed differences in coping and adaptability have also been demonstrated and suggest the potential for improving the fitness of ostriches through selective breeding (Essa & Cloete, 2006; Brand *et al.*, 2007; Engelbrecht *et al.*, 2008).

Genetic line differences in chick survival of young layers have been demonstrated in poultry (Kaiser & Lamont, 2001). Heritability estimates for early and late chick survival in turkey are low to

moderate ($h^2 = 0.02-0.12$) with a low genetic correlation (Quinton *et al.*, 2011). Early studies in poultry reported low heritability estimates for early chick survival, but selective breeding for improved survival has, however, since been shown to be successful in improving survivability in poultry (Morris, 1959; Marble, 1939; Sturkie, 1943; Hutt & Cole, 1947; Morris, 1959; Hu *et al.*, 1997; Beaumont *et al.*, 1999; Ellen *et al.*, 2007).

The ostrich industry can be considered as fairly “young” in the process of domestication. The poultry industry, on the other hand, as evidenced by studies focused on enhanced selection for survival, is much more developed and better established. If the genetic components for survival in ostriches behave the same as the relevant genetic component in poultry, it will be possible to make considerable progress through the genetic selection for enhanced survival. Constituents of survival such as resistance to specific diseases have also been identified to have a notable genetic component in poultry (Guillot *et al.*, 1995; Kaiser *et al.*, 1998; Lamont, 1998; Beaumont *et al.*, 1999; Kaiser & Lamont, 2001). Very little such research has however been done on ratites.

Rearing

Directly after hatching, chicks are maintained in groups of 20-30 for 2-7 days in a controlled environment. Often times the floor may be heated or insulated with a carpet while the ambient temperature is maintained at 30 °C (with oil heaters or asbestos heaters) with adequate ventilation (Verwoerd *et al.*, 1998). In artificial rearing occurs chicks are raised in a control environment. During the course of the day the chicks may have access to a small paddock of kikuyu grass or lucerne (Verwoerd *et al.*, 1998). For the first two weeks post hatch, chicks are brought indoors overnight, thereafter they are maintained in paddocks and provided with shelter (Verwoerd *et al.*, 1998). In an adoption rearing system, chicks are placed with adult foster parents shortly after hatching (Verwoerd *et al.*, 1998). The foster parents together with their adopted chicks are maintained in small paddocks of kikuyu grass or lucerne (Verwoerd *et al.*, 1998).

There is considerable debate regarding which rearing system corresponds with the highest survival (Glatz & Miao, 2008). Both parental condition and incubation have a direct effect on the rearing of ostrich chicks (Verwoerd *et al.*, 1999). All-in all-out systems or mixed groups are two common rearing methods (Glatz & Miao, 2008). Alleged to superior control of the rearing environment, enhanced biosecurity and disease prevention, the all-in all-out rearing system maintains chicks of similar age in one facility for up to 12 weeks (Deeming *et al.* 1996; Verwoerd *et al.* 1999; Black, 2001).

As in other ratites, ostriches have a critical period for chick survival from hatching to 3 weeks post hatch during which time they require special attention (Deeming *et al.*, 1993; Glatz & Maio, 2008). Ostrich chicks are able to run around and find food shortly after hatching and are thus inclined to approach or follow the first prominent visual stimulus that possesses certain simple characteristics, identifying the stimulus as a potential parent (Hess, 1959a; Bateson, 1971; Slagsvold & Hansen, 2008). Chicks therefore form an attachment with any individual present at the time of hatching (Matsushima *et al.*, 2003; Slagsvold & Hansen, 2008). Often irreversible, this attachment is termed filial imprinting and is responsible for a number of the most fundamental animal behaviours and social preferences (Bateson, 1971; Hess, 1959a; Kovach, 1987; Slagsvold & Hansen, 2008). This only occurs during a specific sensitive period early in life that varies between species, stimuli and the environment (Hess, 1959b; Kaufman & Hinde, 1961; Bateson, 1971; Parson & Rogers, 2000; Slagsvold & Hansen, 2008). Improvement in the ability of social animals to forage effectively, manage other resources and avoid predators can arise from observing the prominent imprinting stimulus (Fraser & Broom, 1997). When chicks are imprinted onto a stimulus they will advance towards it and stay in close proximity to that stimulus, manifesting contentment when near to it and anxiety if separated from it (Parson & Rogers, 2000).

The acquisition of certain behaviours, the waning of the inclination to follow and/or the development of fear responses to unfamiliar objects are some factors proposed as effectively concluding the sensitive period during which imprinting may occur (Slagsvold & Hansen, 2008). This phenomenon has been used as a means of environmental enrichment which aims at improving the environment of captive animals, promoting the natural behaviour of chicks and reducing their stress (Newberry, 1995; Reed *et al.*, 1993; Savaterra *et al.*, 1994).

Pivotal to animal welfare, stress is commonly classified as the “non-specific response of an organism to any demand upon it” (Selye, 1973), but most often describes a circumstance that is detrimental to an animal's welfare and should be avoided (Jensen *et al.*, 2008). With stress often playing a significant role in predisposing chicks to elevated mortalities environmental enrichment may comprise a suitable method which may be utilized in enhancing the welfare and subsequent survival of ostrich chicks (Reed *et al.*, 1993; Huchzermeyer 1994; Glatz & Miao, 2008).

Whether the sensitive period specific for imprinting extends to an animal's receptivity to human contact or handling in general, is open to speculation (Kilgour & Dalton, 1984; Jones & Waddington, 1993). There have been several attempts to modify the physiology and behaviour of livestock through regular contact with humans (Hemsworth & Coleman, 1998; Hemsworth & Barnett, 2000). The ontogeny of this phenomenon is however, not well understood and differs

between species (Reed *et al.*, 1993). A number of studies demonstrate regular handling to correspond with a distinct reduction in the degree of anxiety experienced by different species while modelling an effective method for reducing fear of human beings, presumably via habituation (Hughes & Black, 1976; Jones & Faure, 1981; Jones *et al.*, 1991; Jones & Waddington, 1992; Jones, 1992; Hemsworth *et al.*, 1993; Jones & Waddington, 1993; Jones, 1993; Barnett *et al.*, 1994; Hemsworth *et al.*, 1996; Rushen *et al.*, 1999; Zulkifli & Azah, 2004).

There is a delay between hatching and the appearance of fearful behaviour in poultry (Kaufman & Hinde, 1961; Hess, 1959a; Jones & Waddington, 1993). Regular human contact during a stage of lowered fearfulness or the putative sensitive period for imprinting may be beneficial in facilitating a young animal's attachment to human beings (Bolhuis, 1991; Jones & Waddington, 1993).

Fear is an aversive psycho-physiological response to environmental stimuli, which are either novel, encompassing fear-provoking features or are associated with aversive experiences (Suarez & Gallup, 1982; Hemsworth *et al.*, 1994; Boissy, 1995; Jones, 1996; Rushen *et al.*, 1999) bad sentence structure, rephrase. As prey species to varying degrees, domestic animals essentially operate around detecting and escaping predators (Rushen *et al.*, 1999). A fear response ideally motivates animals to evade potentially destructive situations or stimuli (Jones, 1987a; Rushen *et al.*, 1999). In commercial farm industries, however, this response may reduce the welfare of animals and their offspring (Jones & Waddington, 1993). Sudden, unpredictable, intense, prolonged or inescapable elicitation of fear can severely harm the mental and physical wellbeing, growth and reproductive performance of livestock (Jones & Waddington, 1993). Fear reactions such as panic or violent escape are often inappropriate in an intensive farming system and may waste energy and cause feather damage, injury, pain or even death through trampling and smothering (Grandin, 1987; Jones 1989; Mills & Faure 1990; Ewbank, 1993).

Poultry and ostriches startle with sudden changes in their environment and often show panic and violent escape responses when exposed to novel objects such as human beings (Jones 1989). Humans can evoke fear in young domestic animals by aversive handling and by virtue of their relative size, and an inclination towards rapid, erratic movements (Rushen *et al.*, 1999). This is potentially of great importance as elevated or persistent fear of human beings adversely affects the performance, welfare, ease of handling and subsequent management of farm animals (Gross & Siegel, 1982; Rushen & De Passille, 1992). Fearful birds show elevated adreno-cortical and leukocyte responsiveness to stressful stimulation. Chronic elevation of corticosterone depresses performance, while predisposing hens to react more fearfully to distressing events (Beuving & Vonder, 1978; Jones 1989).

The fear of people can, therefore, be a major source of stress in animals, affecting productivity and welfare while potentially inhibiting behavioural systems and generating handling difficulties (Jones & Faure, 1981; Jones, 1989; Mills & Faure, 1990; Jones & Waddington, 1992; Reed *et al.*, 1993; Hemsworth *et al.*, 1994; Rushen *et al.*, 1999). Stress and fear of humans have an adverse effect on growth, maturation, egg production, egg quality, plumage condition and feed conversion efficiency in poultry (Jones & Hughes, 1981; Jones, 1989; Barnett *et al.*, 1992; Jones *et al.*, 1993). Fearful birds may be more active with a higher energy requirement that may be at least partly responsible for the impaired feed conversion of these birds (Hemsworth *et al.*, 1994). Reduced productivity in pigs was also associated with behavioural signs of fear (Rushen *et al.*, 1999). The observed unfavourable relationship between fear and productivity may be an indirect one, but the precise mechanisms are unclear (Hemsworth *et al.*, 1994). In addition, since fear impedes other systems, its adduction is likely to impair the capacity of birds to adjust to environmental modifications, to socialize effectively and to employ novel resources (Jones, 1996). Acute fear is undoubtedly detrimental for the welfare and production of farm animals and its diminution is of foremost importance (Jones, 1996).

Sedation, genetic manipulation, habituation to human handling and environmental enrichment during rearing are some of the methods that may be utilized to amend the fear response of an animal (Reed *et al.*, 1993). Of these methods the influence and implications of human handling and environmental enrichment on the welfare and productivity of animals characterizes an affordable and strategically important structure (Reed *et al.*, 1993; Jones & Waddington, 1993).

Regular handling and environmental enrichment improve the reproductive performance, feed conversion rate, growth, antibody production, disease resistance, mortality and behaviour in a number of different species (Hughes & Black, 1976; Jones *et al.*, 1980; Jones & Hughes, 1981; Gross & Siegel, 1982; Collins & Siegel, 1987; Gvoryahu *et al.*, 1989; Jones, 1989; Jones & Waddington, 1992; 1993; Barnett *et al.*, 1994; Hemsworth *et al.*, 1994). Environmental enrichment and habituation to humans precludes anomalous and often detrimental behaviour, such as aggression, overeating, depression and distress in a variety of livestock species and reduces physiological stimuli associated with drastic changes in the environment that may induce subsequent fear and stress responses (Gross & Siegel, 1982; Collins & Siegel 1987; Jones, 1996; Rushen *et al.*, 1999; Zulkifli & Azah, 2004). Chicks exposed to regular handling and environmental enrichment vocalize, explore and feed more often in a novel environment while exhibiting a reduced avoidance of the experimenter and reduced fear responses (Hess, 1959; Jones *et al.*, 1991; Jones & Waddington, 1993; Reed *et al.*, 1993). The confident behaviour and the elevated levels of environmental pecking exhibited upon exposure to an unfamiliar stimulus may indicate a

greater tendency to employ exploratory rather than fear-related behaviour patterns during environmental change (Gvoryahu *et al.*, 1989; Jones & Waddington, 1993).

Studies on pigs, poultry and dairy cattle have shown that rough or unorthodox handling considerably impacts on an animal's productivity and welfare (Hemsworth *et al.*, 1994; Rushen *et al.*, 1999). Pigs subjected to unorthodox handling have been found to have reduced growth rates, increased age at first oestrus, reduced pregnancy rates, increased age at first mating, reduced litter sizes, and increased litter mortality (Rushen *et al.*, 1999). In contrast, regular unorthodox handling failed to affect the growth of young pigs and poultry (Paterson & Pearce, 1992; Leonard & Fairfull, 1992).

Freeman & Manning (1979) found that handling depresses the growth of layer strain chicks. The effect of handling and environmental enrichment on production and welfare in animals is evidently inconsistent, depending upon an extensive array of influential variables (Rushen *et al.*, 1999). The occasional negative results of studies on the effects of regular handling (Paterson & Pearce, 1992; Kannan & Mench, 1996) show that the relationship between methods of handling, fearfulness and productivity may be highly variable and poorly understood. Continued research is indicated to gain a better understanding of the contributing factors.

Imprinting on humans influences the both the behaviour and performance of ostrich chicks and may impair their future reproductive performance (Bubier *et al.*, 1998). An adoption approach utilizing foster parents may be an effective alternative rearing system that may promote the welfare, survival and performance of ratite chicks while affording less effort and investment for the rearing of the chicks in special facilities (Barri *et al.*, 2005; Janse van Vuuren, 2008; Labaque *et al.*, 1999). Chicks may be reared by foster parents, in a semi-intensive system or intensively. Foster parent rearing is a common practice in South Africa, but necessitates stable weather conditions, substantial breeding stock and foster parents with good nurturing skills who receive new chicks (De Kock 1996; Verwoerd *et al.*, 1999). One adult female can raise up to 25, 0 to 14 day old chicks extensively (Verwoerd *et al.*, 1999) while an adult pair can foster between 30 and 35 chick during colder months and about 60 chicks during warmer months (De Kock 1996). Alternatively, foster parents may be responsible for 100 chicks under semi-extensive conditions with the provision of overnight housing (Glatz & Miao, 2008). Chicks in the care of foster parents may learn feeding behaviour from their parents, as well as benefit from the ingestion of micro-organisms within the parents faeces (Aganga *et al.*, 2003). Rabbits have also been widely used as “dummies” for ostrich chicks, effectively supplementing the mother figure and improving the welfare of the chicks (Madeiros, 1997). Consumption of the rabbit dung by the ostrich chicks provides the chicks with

vitamins B and K while also inoculating the ostrich chicks intestines with beneficial bacteria, preventing yolk sac problems and other diseases associated with poor colonisation of their guts (Madeiros, 1997). Very little research into this form of foster parenting has however been attempted (Madeiros, 1997).

Labaque *et al.* (1999) was concerned that chick mortality may be higher in a foster rearing system than inside an intensive rearing facility. More recent studies have however found those chicks fostered by adult birds exhibit reduced stress and enhanced growth and survival while adult breeder birds are provided opportunity to express natural parental care, enriching the environment of both the chick and the breeder pair (Barri *et al.*, 2005; Janse van Vuuren, 2008; Cloete & Malecki, 2011).

Conclusion

The production of a substantial number of good quality chicks that survive to slaughter must be regarded as one of the most essential components of a breeding program. To date, survival of ostrich chicks has not been subjected to genetic evaluation. Research regarding genetic aspects of ostrich chick survival is scarce, and against this background, the subsequent chapters aim to address these issues.

This thesis therefore focuses on the survival of ostrich chicks during the first 48 weeks post hatch. Fixed effects, genetic parameters, and genetic correlations are described in Chapters 3, 4 and 5, respectively. Chapter 6 comprises a preliminary study comparing foster parenting, human imprinting, regular handling and conventional rearing methods to give more clarity on the potential benefits that it could have for the commercial intensive rearing of ostrich chicks to ensure/improve their survival up to slaughter age.

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Chapter 3

Systematic effects affecting survival to 6 months post hatch in South African Black (*Struthio camelus* var. *domesticus*) ostrich chicks

Abstract

Data from 10418 ostrich chicks hatched in the period from 2000 to 2008 were analyzed to determine the influence of fixed effects upon age specific survival. Age-specific survival was divided into the following intervals: 0 to 1 week survival, 0 to 3 week survival, 0 to 12 week survival, 0 to 24 week survival, 2 to 3 week survival, 4 to 12 week survival and 13 to 24 week survival. ASREML software was used to formulate a fixed effects model for each trait. Storage time only affected 0 to 3 week survival ($P = 0.03$), while incubator type had a significant effect on 0 to 3 week survival ($P = 0.03$), 0 to 12 week survival ($P < 0.001$), 0 to 24 week survival ($P < 0.001$), and 4 to 12 week survival ($P < 0.001$). At older ages (i.e. 0 to 24 weeks, 0 to 12 weeks, 4 to 12 weeks, and 13 to 24 weeks) females exhibited higher survival than males ($P < 0.001$; $P = 0.010$; $P < 0.001$; $P < 0.001$). Hen age was found to have a significant influence on almost all traits (i.e. 0 to 3 week survival, 0 to 12 week survival, 0 to 24 week survival, 2 to 3 week survival and 4 to 12 week survival) except for survival during the first week, and survival from 13 to 24 weeks post-hatch ($P = 0.020$; $P = 0.002$; $P = 0.036$; $P = 0.017$; $P = 0.014$). Exhibiting a significant environmental component, ostrich chick survival to 6 months post-hatch can be optimized by manipulating certain environmental factors like the age of the breeding female as well as the type of incubator used.

Introduction

Low offspring survival particularly during the first few months of life is well documented in ostriches and other ratites, and represents a major obstacle in the industry (More, 1996; Navarro *et al.*, 1998; Cloete *et al.*, 2001; Navarro & Martella, 2002; Glatz & Miao, 2008). Ostrich chicks are predisposed to various infections, diseases, disorders and stresses during the first 3 months post hatch, and mortality recordings commonly range from 10-50% (Allwright 1996; Verwoerd *et al.*, 1997), and around 5-10% from 3 to 6 months post hatch (Verwoerd *et al.*, 1999).

With clearly defined breeding objectives and industry breeding structures largely absent, the potential influence of environmental and genetic factors on ostrich chick survival is unknown (Cloete *et al.*, 2008a). Chick survival is however, recognized as being low and extremely variable

among ostrich flocks (Cloete *et al.*, 2008a). Despite the knowledge that chick management and husbandry have a considerable impact on chick survival, the ideal rearing system is yet to be established (Jensen *et al.*, 1992; Alldredge, 1993; Wade, 1995; Glatz & Miao, 2008).

Environmental and management components may predispose chicks to disease or increase the incidence of diseases in ostrich flocks (Black, 2001). It is thus necessary to understand the impact of such factors on chick survival to make sound management decisions. Estimation of non-genetic parameters that can affect ostrich chick survivability will potentially assist producers in designing or adapting management systems that will optimize the survival of ostrich chicks (Cloete *et al.*, 2002; Brand *et al.*, 2008; Cloete *et al.*, 2008a). Moreover, knowledge of environmental effects on production levels is crucial during genetic evaluation, as biased genetic parameters and breeding values will be derived if such effects are not considered during evaluation.

Against this background, the present study investigated the influence of various environmental effects on the age-specific post-hatching survival of day-old ostrich chicks..

Materials and methods

Experimental location

A resource population from the Oudtshoorn Experimental farm, Oudtshoorn, South Africa provided pedigree and performance data. Situated in the Klein Karoo area of the Western Cape Province, Oudtshoorn has a Mediterranean climate with an annual rainfall of between 200 and 300mm per year.

Resource population

South African Black ostrich pedigree and performance data recorded from 2000 to 2008 on the Oudtshoorn Experimental Farm, South Africa were utilised. Bred for improved feather quality, the South African Black ostrich stems from crosses between the North African subspecies (*S. c. camelus*) and wild southern African subspecies (*S. c. australis*) and is the primary species around which much of the South African ostrich industry was established (Engelbrecht *et al.*, 2008). In the 1980s, commercial pair-breeding birds were donated to the Oudtshoorn Research Farm, followed by further additions to the flock in the 1990s. From these birds' commercial and feather founder parent strains were established, with the feather birds being selected purely on those birds displaying better feather qualities (Bunter & Cloete, 2004). With the majority of the breeders being

selected from within the flock, the 63 pairs in 1991 gradually developed to 136 pairs in 2000 and 188 pairs from 2003. The data recorded from 2000 to 2008 represented the progeny of 378 females and 387 males, from which 10418 chicks were hatched. The separate breeding pairs, each with known identifies are maintained in breeding camps of approximately 0.25 ha each to ensure accurate pedigree and performance recordings.

Management

Eggs were collected on a daily basis, identified, stored (Van Schalkwyk *et al.*, 1999) and subsequently set in artificial incubators every Tuesday. Although the incubators were of different manufacturers, they were all maintained at a relative humidity of 24% and a temperature of 36°C. Incubators were set to turn the vertically set eggs hourly through either a 60° or 90° angle. After 35 days of artificial incubation, eggs were transferred to hatchers, where they were incubated for the remainder of the incubation period at a relative humidity of 28%, and a temperature of 36°C. During the last week of incubation, eggs were incubated in a vertical position, with no turning being performed. The day and time (from 8:00 to 16:30, constituting normal working hours) that external pipping occurred was recorded, and the eggs were then moved to the dry-off hatcher. Here the eggs were placed in separate compartments such that their identities were known. Those eggs that did not hatch on the 43rd day of incubation, were candled, checked for signs of life and subsequently assisted to hatch when needed.

Chicks hatched were left to dry off for a maximum of 24 hours before they were weighed, sexed and fitted with a temporary identity tag on the left wing. After the disinfection of the navels, chicks were relocated to an intensive rearing facility where they were kept indoors for a week. The ambient temperature was gradually decreased from 30°C to 25°C. A pre-starter diet was made available to the chicks *ad libitum*. For the first week, lucerne clippings were sprinkled on top of the feed every morning to encourage eating. Biovit water was made available in water dispensers from 7am to 4pm every day. After the first week, chicks were generally allowed to browse lucerne pastures. The broods comprised of one to several hatching groups of between 80 and 150 chicks up to 3 months of age. When the birds reached approximately 18kg live weight, their diet was changed to a crumbed Starter diet containing 190g crude protein and 11.5MJ metabolisable energy per kg of diet. Once the chicks attained a live weight of 36kg at approximately 3 months after hatch they were transferred to a feedlot, where they were maintained to slaughter. Birds were before being transferred to the feedlot, fitted with a permanent identity tag on their necks and fed a grower diet containing 155g crude protein and 10.5MJ metabolisable energy per kg of diet. Once the chicks reached between 6 and 10 months of age, the groups were divided to comply with

guidelines on the stocking density for slaughter birds. Groups of chicks that hatched early in the breeding season and had good growth rates were kept as potential replacement breeding birds. Any mortalities were recorded on a daily basis.

Data editing

The initial data included information pertaining to the dam identity, sire identity, production year, season, date of lay, date of setting, date of pipping, time of external pipping, incubator type, day-old chick weight, egg weight on day of production, egg weight at 21 days of incubation, egg weight at 35 days of incubation, age of dam, age of sire, mortality date, and mortality age. From this, the duration of storage, and the moisture loss at 35 days of incubation were calculated. The data recorded in Microsoft Excel (2007) was exported to a spreadsheet format compatible with the Statistical Analysis System (SAS, 2004). Utilizing SAS Enterprise Guide 4, one-way frequency procedures were executed to allow a general overview of the data. The distribution and range of the various components were analyzed. Only those chicks hatching within the breeding season, from winter to summer were. A total of 896 out of 11314 records contained extreme outliers that skewed the normal distribution of the data or included missing values and were thus removed from the analyses. Eggs stored for longer than 7 days were grouped together. Where dam age or sire age exceeded 11 years, a group of 11+ years was created. .

Survival intervals

A Microsoft Excel 2007 pivot graph (Figure 3.1) showing the mortality curve relative to age of chicks was created. The curve corresponded closely to that depicted by Cloete *et al.*, (2001). This graph together with the general time-specific management practices and the physiological changes of the ostrich chicks were utilized to determine age specific survival traits to be analyzed.

For the first week post hatch, while learning to eat, ostrich chicks are supplemented by the yolk sac. The exact rate at which the yolk sac is absorbed by a young ostrich chick is not yet established, with estimates varying from 7-10 days to 2-3 weeks (Smit, 1963; Jensen *et al.*, 1992; Verwoerd *et al.*, 1999). Yolk lipids provide the primary source of energy for the embryo and young chick, and the differences in yolk composition and size may be associated with hatchling health and survival (Estaban *et al.*, 1991; Bunter, 2002; Fassenko, 2008).

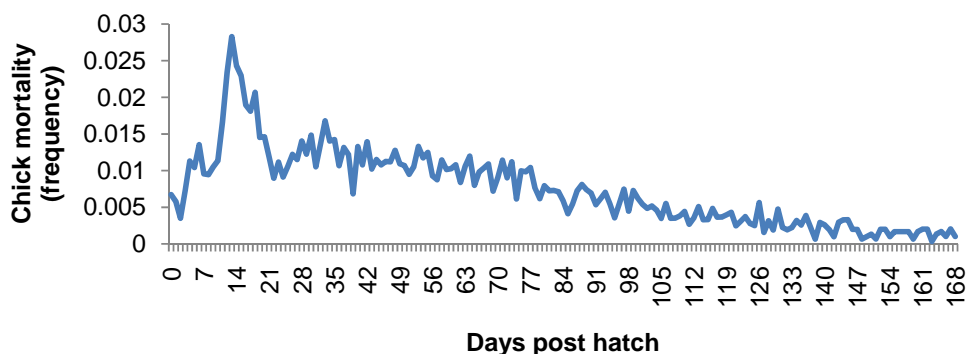


Figure 3.1 The frequency of age specific ostrich chick mortality to the total number of chicks alive

Management practices on the Experimental farm are such that ostrich chicks are relocated at 4 weeks and 12 weeks post hatch. This corresponds with a change in diet that occurs at approximately the same time, depending on the weight of the individual chick.

The following survival intervals were thereafter determined for analysis:

- 0 to 1 week survival (0-1WKS), comprising of 10418 records.
- 0 to 3 week survival (0-3WKS), comprising of 10418 records.
- 0 to 12 week survival (0-12WKS), comprising of 10418 records.
- 0 to 24 week survival (0-24WKS), comprising of 10418 records.
- 2 to 3 week survival (2-3WKS), comprising of 9729 records (i.e. including only those chicks that were alive at 2 weeks post hatch).
- 4 to 12 week survival (4-12WKS), comprising of 7022 records (i.e. including, only those chicks that were alive at 4 weeks post hatch).
- 13 to 24 week survival (13-24WKS), comprising of 3886 records (i.e. including, only those chicks that were alive at 4 weeks post hatch).

Estimation of fixed effects

The contribution of the fixed effects on the fitted model for each survival trait was analyzed by means of a series of single-trait binomial analyses in ASREML (Gilmour *et al.*, 2009). Those effects with a p-value of less than 0.05 were subsequently included in the operational models for further analyses. Subsequent to the establishment of the importance of the various fixed effects, least-squares means were calculated by means of the ASREML statistical package (Gilmour *et al.*, 2009).

The fixed effects model for the survival traits was

$$Y_{ijklmgq} = \mu + S_i + B_j + O_{kl} + D_m + F_g + P_{ql} + e_{ijklmg}$$

Where:

$Y_{ijklmgq}$ = age-specific survival

μ = population mean

S_i = fixed effect of the i^{th} sex ($i = 1, 2$) (male/female)

B_j = fixed effect of the j^{th} incubator ($j = 1, 3, 4, 2, 5$)

O_{kl} = interaction effect of the l^{th} hatching season in the k^{th} year (winter, spring, summer; 2000-2008)

D_m = fixed effect of the m^{th} dam age ($m = 2, 3, 4 \dots 11+$)

F_g = fixed effect of the g^{th} storage time ($t = 1, 2, 3 \dots 7+$)

P_{ql} = fixed effect of the q^{th} rearing group nested in the l^{th} year

e_{ijklmg} = random error

ASREML software was utilized to run single-trait analyses on age-specific mortality so that suitable fixed effects models could be developed. Fixed effects fitted were hen age (2 to 11+ years), year of hatch (2000 to 2008), hatching season (winter, spring and summer), storage time prior to setting (1 to 8+ days), rearing group and incubator.

Results and Discussion

Descriptive statistics for the data are presented in Table 3.1. Considered as a binomial trait, survival traits equaling zero represent those chicks that died, while one denotes those chicks that survived to the specified time. The coefficients of variation for survival traits ranged from 26.62% to 159.90%. There is an appreciable decline in the number of records with time, as a result of mortalities occurring during the post-hatching phase (Figure 3.1).

Survival was highest at 93% to the end of the first week post hatching, but declined to 73% after 3 weeks, and 37% after 12 weeks. This decline in survival may be partly explained by the physiological changes occurring at this time. Directly after hatching, the yolk sac functions as a food source for the chick during the first 4-6 days post hatch (Dzoma & Dorrestein, 2001; Aganga *et al.*, 2003), and has a vital role to play in complementing the absorption of nutrients, ensuring rapid growth of the chick (Murakami *et al.*, 1992). Between 10 and 13 days after hatch the yolk is normally completely utilised, becoming a sacculum of varying size containing a very small cavity

devoid of yolk, which is ultimately converted to scar tissue (Dzoma & Dorrestein, 2001; Mushi *et al.*, 2004). By this time, chicks should be eating adequately to maintain typical growth and development. However inadequate feeding behaviour associated with low feed ingestion may be responsible for an increased number of mortalities at this stage (Aganga *et al.*, 2003; Brand & Olivier, 2011). Once chicks attain 3 months of age they are usually hardy, only requiring shelter from inclement weather, and survival tends to stabilize at a higher rate (75%) (Glatz & Miao, 2008).

Table 3.1 Descriptive statistics for age specific survival traits (0 to 1 week survival (0-1WKS), 0 to 3 week survival (0-3WKS), 0 to 12 week survival (0-12WKS), 0 to 24 week survival (0-24WKS), 2 to 3 week survival (2-3WKS), 4 to 12 week survival (4-12WKS) and 13 to 24 week survival (13-24WKS)) recorded during the 2000 to 2008 breeding seasons.

Trait	Records	Mean	Coefficient of variation
0-1WKS	10418	0.93 (0.25)	26.61
0-3WKS	10418	0.73 (0.44)	61.01
0-12WKS	10418	0.37 (0.48)	129.66
0-24WKS	10418	0.28 (0.45)	159.90
2-3WKS	9729	0.92 (0.28)	30.13
4-12WKS	7022	0.55 (0.50)	89.84
13-24WKS	3886	0.75 (0.43)	57.17

The respective fixed effects models calculated for each of the age specific survival traits are depicted in Table 3.2. The interaction of year with hatching season had a significant effect upon chick survival during the first 6 months post hatch ($P < 0.001$ and $P < 0.005$, respectively). The combined effect of rearing group and year exhibits a P-value of < 0.005 for all age specific survival traits, except for the interval of 13 to 24 weeks post hatch. Storage time had a significant effect only for the period from 0 to 3 week after hatching. The effect of the gender of chicks on survival only became apparent at later ages with females outperforming males. The age of the hen had a significant effect on all age-specific survival traits (0-3WKS: $P = 0.036$, 0-12WKS: $P = 0.002$, 0-24WKS: $P = 0.020$, 2-3WKS: 0.017) except during the first week post hatch and from 13 to 24 weeks post hatch.

Table 3.2 P-values of the respective fixed effects of age specific survival traits of ostrich chicks recorded during the 2000 to 2008 breeding seasons (ns=not significant). Fixed effects were sex (SEX-2 levels; male, female), hen age (HAGE-11 levels; 2 to 11+ years), year (YR-9 levels; 2000 to 2008), hatching season (HS-3 levels; Winter, Spring and Summer), storage time (STIME-0 to 7+ days), rearing group (RGR-32 levels) and incubator (INC-1;2;3;4;Combination; as defined by Brand *et al.*, 2009)

Trait	SEX	INC	YR.HS	HAGE	STIME	RGR.YR
0-1WKS	ns	ns	<0.001	ns	ns	0.005
0-3WKS	ns	0.030	<0.001	0.036	0.032	<0.001
0-12WKS	0.010	<0.001	<0.001	0.002	ns	<0.001
0-24WKS	<0.001	<0.001	<0.001	0.020	ns	<0.001
2-3WKS	ns	ns	<0.001	0.017	ns	<0.001
4-12WKS	<0.001	<0.001	<0.001	0.014	ns	<0.001
13-24WKS	<0.001	ns	<0.001	ns	ns	ns

Table 3.3 Least-squares means depicting the age specific survival (\pm s.e.) of male and female ostrich chicks recorded during the 2000 to 2008 breeding seasons.

Trait	Male	Female
0-1WKS*	0.94 \pm 0.003	0.93 \pm 0.004
0-3WKS*	0.74 \pm 0.006	0.72 \pm 0.006
0-12WKS	0.36 \pm 0.007	0.38 \pm 0.007
0-24WKS	0.27 \pm 0.006	0.30 \pm 0.006
2-3WKS*	0.92 \pm 0.006	0.91 \pm 0.006
4-12WKS	0.53 \pm 0.008	0.57 \pm 0.008
13-24WKS	0.73 \pm 0.010	0.77 \pm 0.009

*traits unaffected by the sex of the chick

The fixed effect of gender of age-specific chick survival

Gender had no effect on early chick survival. This reflects the findings of Cloete *et al.* (2001). At later ages, however, the female birds exhibited an improved survival (77% for females and 73% for males: Table 3.3). Males are generally more susceptible to disease which may explain their reduced survival (Klein, 2000). As the birds get older, the significance of the sex effect may also correspond to elevated disparity in the general behaviour and/or temperament of the sexes as well as to physiological variation between genders and susceptibility to injury and disease.

The fixed effect of incubator type on age specific survival

All those chicks that hatched from incubator 4 died after the first week post hatch (Table 3.4). This finding corresponds with Cloete *et al.* (2001) who found chicks hatching from eggs incubated in incubator 4 had elevated 28 day mortalities. The combination of incubators exhibited a superior chick survival for all traits where incubator type was significant. In contrast, Brand *et al.* (2007) reported that such eggs were more likely to sustain embryonic mortalities. The cumulative effect of unsatisfactory incubator conditions specific to an incubator for a particular egg may be avoided by transferring the eggs between the incubators. Despite the fact that the incubators are set at the same specific relative humidity and temperature, the absolute humidity and temperature that surrounds the eggshell may vary depending on the design of the incubator and the ambient conditions inherent to the particular incubator (Brand *et al.*, 2008). If eggs are exposed to stress during incubation and the chicks do not hatch under optimal conditions, there is a high probability that they will not survive (Glatz & Miao, 2008).

Table 3.4 Mean survival (\pm s.e.) of ostrich chicks per incubator for 0 to 1 week survival (0-1WKS), 0 to 3 week survival (0-3WKS), 0 to 12 week survival (0-12WKS), 0 to 24 week survival (0-24WKS), 2 to 3 week survival (2-3WKS), 4 to 12 week survival (4-12WKS) and 13 to 24 week survival (13-24WKS) recorded during the 2000 to 2008 breeding seasons.

Trait	INC 1	INC 2	INC 3	INC 4	COMB.
0-1WKS*	0.94 \pm 0.003	0.90 \pm 0.005	0.93 \pm 0.018	0.87 \pm 0.071	0.90 \pm 0.019
0-3WKS	0.74 \pm 0.005	0.68 \pm 0.009	0.71 \pm 0.028	0	0.79 \pm 0.026
0-12WKS	0.37 \pm 0.006	0.24 \pm 0.010	0.39 \pm 0.025	0	0.46 \pm 0.031
0-24WKS	0.27 \pm 0.005	0.20 \pm 0.009	0.32 \pm 0.024	0	0.36 \pm 0.30
2-3WKS*	0.78 \pm 0.005	0.77 \pm 0.009	0.76 \pm 0.027	0	0.88 \pm 0.022
4-12WKS	0.55 \pm 0.007	0.58 \pm 0.012	0.37 \pm 0.035	na	0.62 \pm 0.035
13-24WKS*	0.73 \pm 0.009	0.82 \pm 0.012	0.84 \pm 0.045	na	0.78 \pm 0.038

*traits unaffected by the incubator type

Interaction of hatching season within year on age-specific chick survival

Ostriches are most commonly considered seasonal breeders (Deeming & Ar, 1999). The peak production season of ostriches in the southern hemisphere occurs between July and January (Lambrechts, 2004). With variations in environmental temperature, humidity and air circulation, variation in the number of mortalities between years is to be expected. Across years however, those chicks that hatch in winter had the highest survival for all ages extending beyond the first

week post hatch. This is followed closely by summer for the early survival, but for survival from 4 to 12 weeks, no difference between winter and spring was observed, while chicks hatching in spring outperformed chicks hatching in summer for 13 to 24 weeks survival. According to Verwoed *et al.* (1999) chicks hatching later in the season incline towards a reduced survival. Glatz & Miao (2008) found the hatchability of eggs to decrease with the advancement of the season. Cloete *et al.* (2001), however, found 28 day mortalities to be greatest for eggs hatching in winter and summer.

The fixed effect of age of the dam on age specific chick survival

Two year-old dams correspond with a reduced survival for chicks older than a week. Chick survival for older chicks stabilises for dams between 3 and 9 years of age, increasing for dams 10 years and older. Early chick survival on the other hand is consistent for all ages of dams. The age of the female ostrich is known to influence the number of eggs laid, the egg weight and therefore the day old chick weight (Majewksa, 2001; Bunter & Cloete, 2004; Lambrechts, 2004; Brand *et al.*, 2008). A female generally starts laying at between 2 and 2.5 years of age, attaining her peak production when between 8 and 9 years old (Brand *et al.*, 2007). As the birds get older, the number of eggs they produce per season, their fertility and the hatchability of the eggs all increase up to a point (Ipek & Sahan, 2004). However, beyond that, eggs produced by the older breeders are characterised by an increased number of embryonic mortalities and a higher likelihood to produce under-grade chicks (Boerjan, 2002; Tona *et al.*, 2004; Brand *et al.*, 2007). The results presented here may however, exhibit a slight bias as those birds older than 11 years were grouped together as a result of the variability and general reduction in the number of dams older than 11 years.

Table 3.5 Mean survival (\pm s.e.) of ostrich chicks per age of hen (years) for 0 to 1 week survival (0-1WKS), 0 to 3 week survival (0-3WKS), 0 to 12 week survival (0-12WKS), 0 to 24 week survival (0-24WKS), 2 to 3 week survival (2-3WKS), 4 to 12 week survival (4-12WKS) and 13 to 24 week survival (13-24WKS) recorded during the 2000 to 2008 breeding seasons.

Trait	2YR	3YR	4YR	5YR	6YR	7YR	8YR	9YR	10YR	11+YR
0-1WKS*	0.95 \pm 0.010	0.92 \pm 0.007	0.94 \pm 0.006	0.94 \pm 0.006	0.94 \pm 0.006	0.93 \pm 0.007	0.93 \pm 0.009	0.94 \pm 0.009	0.92 \pm 0.013	0.91 \pm 0.015
0-3WKS	0.66 \pm 0.020	0.75 \pm 0.012	0.73 \pm 0.011	0.72 \pm 0.011	0.75 \pm 0.012	0.70 \pm 0.013	0.77 \pm 0.014	0.73 \pm 0.018	0.68 \pm 0.023	0.79 \pm 0.022
0-12WKS	0.31 \pm 0.020	0.38 \pm 0.013	0.38 \pm 0.012	0.37 \pm 0.011	0.38 \pm 0.013	0.34 \pm 0.013	0.37 \pm 0.016	0.37 \pm 0.019	0.33 \pm 0.023	0.58 \pm 0.026
0-24WKS	0.23 \pm 0.018	0.28 \pm 0.012	0.30 \pm 0.011	0.28 \pm 0.011	0.29 \pm 0.012	0.24 \pm 0.012	0.27 \pm 0.015	0.27 \pm 0.018	0.25 \pm 0.021	0.44 \pm 0.023
2-3WKS	0.69 \pm 0.020	0.81 \pm 0.011	0.78 \pm 0.010	0.77 \pm 0.010	0.80 \pm 0.011	0.75 \pm 0.012	0.82 \pm 0.014	0.78 \pm 0.017	0.73 \pm 0.02	0.87 \pm 0.022
4-12WKS	0.52 \pm 0.028	0.54 \pm 0.016	0.55 \pm 0.015	0.56 \pm 0.014	0.55 \pm 0.016	0.53 \pm 0.017	0.53 \pm 0.021	0.54 \pm 0.024	0.53 \pm 0.030	0.75 \pm 0.026
13-24WKS*	0.76 \pm 0.033	0.74 \pm 0.020	0.79 \pm 0.016	0.76 \pm 0.016	0.77 \pm 0.018	0.71 \pm 0.022	0.75 \pm 0.025	0.74 \pm 0.029	0.75 \pm 0.037	0.76 \pm 0.030

*traits unaffected by the age of the female

Table 3.6 Mean survival (\pm s.e.) of ostrich chicks per storage time for 0 to 1 week survival (0-1WKS), 0 to 3 week survival (0-3WKS), 0 to 12 week survival (0-12WKS), 0 to 24 week survival (0-24WKS), 2 to 3 week survival (2-3WKS), 4 to 12 week survival (4-12WKS) and 13 to 24 week survival (13-24WKS) recorded during the 2000 to 2008 breeding seasons.

Trait	1 DAY	2 DAY	3 DAY	4 DAY	5 DAY	6 DAY	7+ DAY
0-1WKS*	0.92 \pm 0.007	0.94 \pm 0.006	0.93 \pm 0.007	0.94 \pm 0.006	0.93 \pm 0.006	0.93 \pm 0.007	0.94 \pm 0.007
0-3WKS	0.70 \pm 0.012	0.75 \pm 0.011	0.73 \pm 0.011	0.74 \pm 0.012	0.73 \pm 0.011	0.73 \pm 0.012	0.74 \pm 0.012
0-12WKS*	0.37 \pm 0.013	0.39 \pm 0.013	0.38 \pm 0.013	0.37 \pm 0.013	0.37 \pm 0.012	0.37 \pm 0.013	0.37 \pm 0.013
0-24WKS*	0.29 \pm 0.012	0.29 \pm 0.012	0.29 \pm 0.012	0.27 \pm 0.012	0.28 \pm 0.012	0.27 \pm 0.012	0.27 \pm 0.012
2-3WKS*	0.75 \pm 0.0116	0.80 \pm 0.011	0.78 \pm 0.011	0.78 \pm 0.011	0.78 \pm 0.011	0.78 \pm 0.011	0.78 \pm 0.011
4-12WKS*	0.58 \pm 0.016	0.56 \pm 0.015	0.57 \pm 0.016	0.54 \pm 0.016	0.55 \pm 0.015	0.54 \pm 0.016	0.54 \pm 0.016
13-24WKS*	0.78 \pm 0.018	0.75 \pm 0.018	0.78 \pm 0.017	0.74 \pm 0.019	0.76 \pm 0.018	0.73 \pm 0.020	0.74 \pm 0.020

*traits unaffected by the duration of storage prior to setting

Effect of egg storage time on age specific chick survival

The length of storage prior to setting had a negligible effect for most survival traits. The storage time abridges the time period between collection of the eggs from the breeder camps and setting of the eggs in the incubator. Ideally ratite eggs should not be stored for longer than 7 days prior to incubation (Stern, 1991; Brand *et al.*, 2007). Once storage time exceeds 7 days, embryonic abnormalities and mortalities rise with a subsequent decrease in hatchability, an extended incubation period and an elevated frequency of poor-quality chicks (Deeming, 1996; 1997; Ar & Gefen, 1998; Boerjan, 2002; Fassenko *et al.*, 2002; Tona *et al.*, 2003; Decuyper & Bruggeman, 2007). In this study, eggs were mostly stored for less than 7 days and set in weekly intervals. This may be the reason for the negligible effect of the duration of the egg storage on chick survival for most traits.

Conclusion

Ostrich chick survival to 6 months post hatch exhibits a great degree of variation, with a significant environmental component. Certain aspects like the unpredictable changes between year-season combinations are uncontrollable. For optimal survival to be achieved, one should breed chicks from dams of between 2 and 9 years of age to hatch primarily in the winter months. Further research into the components of ideal artificial incubation and chick rearing practices as well as genetic parameters of survival should be undertaken. The production of robust chicks that have an increased probability to survive could possibly result from a better understanding of these multiple interacting factors.

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Chapter 4

Genetic parameters for chick survival to 6 months post hatch in South African Black ostriches (*Struthio camelus* var. *domesticus*) using linear, mixed methods

Abstract

Data recorded on ostrich chicks were used to estimate genetic parameters for age specific post hatching survival from 0 to 1 week survival, 0 to 3 week survival, 0 to 12 week survival, 0 to 24 week survival, 2 to 3 week survival, 4 to 12 week survival and 13 to 24 week survival. Three-trait analyses included incubation moisture loss to 35 days incubation, day of external pipping and day-old chick weight estimated correlations with cumulative survival traits to 1 week, 3 weeks and 12 weeks post hatch. An animal model utilizing data of up to 10418 chick records from a commercial pair bred ostrich flock in Oudsthoorn, South Africa was utilized. Heritability estimates for all survival traits were low at respectively, 0.06, 0.05, 0.08, 0.01, 0.07, 0.05 and 0.04 in the single-trait analyses. Three-trait analyses exhibited similar heritability estimates. Only 0 to 1 week survival had a significant maternal component (0.03), while 4 to 12 week survival was influenced by a dam permanent environmental effect (0.02). Early (<3 months) ostrich chick survival exhibited significant genetic variation, albeit low. Ostrich chick survival to 6 months post hatch also demonstrated low levels of genetic variation. Neither moisture loss nor day of external pipping exhibited notable genetic correlations with any of the estimated survival traits. Day-old chick weight is lowly correlated with early chick survival with heavier chicks tending to have a higher survival probability. Further research is required to ascertain how the significant genetic variation may be exploited to improve chick survival.

Introduction

The ostrich industry lacks distinct breeding objectives and breeding structures, while environmental and genetic influences for some key traits are unknown (Cloete *et al.*, 2008). Non-genetic effects and genetic parameters as well as responses to selection for specific traits need to be determined for the definition of appropriate breeding objectives (Cloete *et al.*, 2002; Brand *et al.*, 2008a; Cloete *et al.*, 2008). The most fundamental discrepancy pertaining to genetic parameters for performance or reproductive traits of ostriches is a lack of accurate genetic parameters for chick survival (Cloete *et al.*, 2008). High and variable chick mortalities, predominantly during the first few months post

hatch, represent a major challenge for the industry (Cloete *et al.*, 2001). Ostrich chicks are predisposed to various infections, diseases, disorders and stresses during their first 3 months post hatch and survival recordings commonly range from 10-50% (Allwright 1996; Verwoerd *et al.*, 1997) and around 5-10% from 3 to 6 months post hatch (Verwoerd *et al.*, 1999). More systematic studies of chick survival would assist in the development of adapted breeding and husbandry systems that reduce stress imposed on chicks while enhancing the coping ability and resistance of the chicks. Chick survival and the commercial production of ostriches could thus be improved (Verwoerd *et al.*, 1999).

Relationships between different traits are mandatory for the prediction of the direction and extent of the correlated responses expected to occur when trait specific selection is undertaken (Falconer, 1960). Correlations among incubation traits (Brand *et al.*, 2008a), live weight traits (Bunter & Cloete, 2004) and other production and reproduction traits (Cloete *et al.*, 2008) are readily available in the ostrich industry. No such correlations or estimates pertaining to chick survival have, however, been reported. Additional knowledge of the genetic and environmental factors affecting chick mortality, as well as correlations with traits recorded during the last week of incubation or soon after hatching would be of assistance in the development of breeding plans that could possibly enhance the survival and subsequent performance of ostrich chicks.

Against this background, this chapter focuses on the levels of genetic variation in age-specific chick survival in a commercial South African (SA) Black ostrich breeding flock. Both linear models and threshold models employing Gibbs sampling were used to estimate respective variance and (co)variance components. Attention was divulged to both early (<3 months post hatch) and late (3-6 months post hatch) chick survival.

Materials and Methods

Description of the data

A commercial pair-bred ostrich flock maintained at the Oudtshoorn Research Farm, South Africa formed the base population, providing the pedigree and performance data for the present study. South African Black ostrich (*Struthio camelus* var. *domesticus*) data recorded from 2000 to 2008 were used. The pedigree file involved 13073 individuals over 6 generations that were the progeny of 387 sires and 378 dams. The management of the breeding pairs and the eggs has previously been discussed in Chapter 3 as well as in the literature (Bunter & Cloete, 2004; Brand *et al.*, 2007; Cloete *et al.*, 2008).

Traits Recorded

The definitions of age specific survival traits have been discussed in Chapter 3. The following traits were analysed (traits in bold font were utilized in the multi-trait analyses) (See Table 3.1):

- **0 to 1 week survival (0-1WKS), comprising of 10418 records**
- **0 to 3 week survival (0-3WKS), comprising of 10418 records**
- **0 to 12 week survival (0-12WKS), comprising of 10418 records**
- 0 to 24 week survival (0-24WKS), comprising of 10418 records
- 2 to 3 week survival (2-3WKS), comprising of 9729 records, only including those chicks that were alive at 2 weeks post hatch
- 4 to 12 week survival (4-12WKS), comprising of 7022 records, only including those chick that were alive at 4 weeks post hatch
- 13 to 24 week survival (13-24WKS), comprising of 3886 records, only including those chicks that were alive at 13 weeks post hatch
- **Incubation moisture loss at 35 days incubation (ML35)**
- **Day of external pipping (PKDAY)**
- **Day old chick weight (DOCW)**

Development of statistical method

Systematic effects

A sequence of analyses executed in Chapter 3 determined the important systematic effects for each of the survival traits (Table 3.1). These systemic effects were therefore included in respective operational models for each of the traits. Genetic parameters for incubation traits incorporated into the multi-trait analyses have been documented previously and were therefore not considered in Chapter 3 (Bunter & Graser, 2000; Bunter & Cloete, 2004; Brand & Cloete, 2006; Brand *et al.*, 2008a, Brand *et al.*, 2009).

Random effects

An animal model ascribing every record to an individual was utilized in the estimation of the variance components for age-specific survival traits. The maternal genetic (m^2) and maternal permanent environment (c^2) were fitted additionally to model the maternal effects of the hen. The following general model formulation was utilized for the analysis of the each trait:

$$y_{ij} = X\beta + e_{ikj} \quad (\text{Model 1})$$

$$y_{ij} = X\beta + Z_1a_i + e_{ikj} \quad (\text{Model 2})$$

$$y_{ij} = X\beta + Z_1a_i + Z_3pe_j + e_{ikj} \quad (\text{Model 3})$$

$$y_{ij} = X\beta + Z_1a_i + Z_2m_j + e_{ikj} \quad (\text{Model 4})$$

$$y_{ij} = X\beta + Z_1a_i + Z_2m_j + Z_3pe_j + e_{ikj} \quad (\text{Model 5})$$

Where

y_{ij} is an observation for the i^{th} chick of the j^{th} hen

$X\beta$ is an incidence matrix associating the records with the appropriate fixed effects

Z_1 is an incidence matrix associating records to the direct additive genetic effects

Z_2 is an incidence matrix associating records to the maternal additive genetic effects

Z_3 is an incidence matrix associating records to the maternal permanent environmental effects

a_i is the vector for the additive genetic effect

m_j is the vector for the maternal genetic effect

pe_j is the vector for the maternal permanent environmental effect

e_{ikj} is the vector for the residual effects

The animal model utilized designated:

$$Var(a) = A\sigma_a^2; Var(m) = I\sigma_m^2; Var(pe) = I\sigma_{pe}^2 \text{ and } Var(e) = I\sigma_e^2$$

Where

A is a matrix relating the associations between animals (i.e., the Numerator Relationship Matrix)

I is the identity matrix

σ_a^2 is the variation attributed to the additive genetic effect

σ_m^2 is the variation attributed to the maternal genetic effect

σ_{pe}^2 is the variation attributed to the maternal permanent environmental effect

σ_e^2 is the residual variation

Statistical procedures

Single-trait analyses

Subsequent to the careful editing of data described in Chapter 3, ASREML software (Gilmour *et al.*, 2009) was utilized to run single-trait analyses on age-specific survival so that suitable fixed and random effects models could be developed. Initially binomial survival data was transformed using a

logit transformation. The results proved to be very similar to when survival data was treated as normally distributed, and the latter approach was preferred for simplicity of presentation. Random effects fitted sequentially included additive animal effects, maternal genetic effects and dam permanent environmental effects (fitted as unique dam across years). The pair-mating structure in ostriches lead to high sampling correlations between random effects, but it was still possible to partition the random effects that were considered, as was also reported by Bunter & Cloete (2004). Likelihood Ratio tests (LRT) together with their corresponding sums of squares (s^2) were used to determine which random terms significantly contributed to the respective traits. The LRT tests the increase in Log-likelihood resulting from the addition of random term to the model of analysis (starting with model 1). When two models incorporated an equal number of random terms, that model with the highest log-likelihood value was chosen. The corresponding variance components were estimated. Average information algorithms concomitantly supplied standard error estimates for the derived genetic parameters, as described by Gilmour *et al.* (2009).

Multi-trait analyses

Models developed under the single-trait analyses of survival traits were utilized for the multi-trait analyses. Supplementary single-trait analyses were performed for ML35, PD and DOCW in the same manner described above, and as reported by Wang *et al.* (2011). The most suitable models were then selected for the multi-trait analyses. Heritability estimates acquired in the single-trait analyses suggested close correspondence between parameters derived for certain age-specific survival traits. It was hence decided to only employ cumulative age-specific survival traits up to 12 weeks post hatch together with incubation traits. Two-trait analyses allowed the estimation of the appropriate correlations between traits. It was subsequently decided to perform three-trait analyses including two of the defined incubation traits (ML35, PD and DOCW) with each of the cumulative survival traits per analyses. The appropriate correlations were obtained from these analyses and presented in the results. All analyses were performed utilizing ASREML software (Gilmour *et al.*, 2006).

Results and discussion

Single-trait analyses

The log-likelihood values and their residual mean squares (s^2) were utilized to determine the most suitable model for each trait (Table 4.1). Only survival during the first week post hatch exhibited a significant improvement in the log-likelihood value with the inclusion of the additive maternal

component (9109.46 to 9115.97). Four to 12 week survival was affected by dam permanent environmental effects, with log likelihood values increasing from 1990.15 to 1992.08. No improvement in the log-likelihood values for 2-3WKS and 13-24WKS was apparent with the inclusion of maternal effects.

Random effects: The estimates of the genetic parameters for each of the traits together with their standard errors are represented in Table 4.2.

The derived heritability estimates for all traits were low, but were mostly higher than double the corresponding standard error. Selection for an improved survival within the first 3 months post hatch could thus benefit average flock performance. No previous studies on the heritability of chick survival were found to relate these results to. However, early studies on chickens suggested heritability estimates of the same magnitude for post-hatching survival (see review by Kinney, 1969). It is conceded that survival data at later ages were severely censored, which could have masked some genetic variation.

Survival within the first week post hatch appeared to have a negligible animal additive effect (fitted as default in this case). The additive maternal effect, however, played a more distinct role, albeit small in magnitude. Physical properties of the egg/eggshell, internal embryonic factors and subsequent moisture loss by the egg during incubation all determine the quality of the chick that hatches (Ar *et al.*, 1996; Adewumi *et al.*, 2008; Brand *et al.*, 2008a). Dzailowski & Sotherland (2003) found that the morphology and physiology of Emu hatchlings was significantly correlated with the maternal investment in the offspring, specifically through egg size and egg composition. Aspects like yolk quality could also have contributed as chicks can survive for approximately a week on the nutrients contained in the yolk (Dzoma & Dorrestein, 2001). It is thus reasonable to attribute the success of the chicks during the first days after hatch to such maternally induced traits. The significant maternal contribution to early post hatching survival is therefore not entirely unexpected.

Table 4.1 Loglikelihood ratios (residual mean square) for each the respective models fitted to 0 to 1 week survival (0-1WKS), 0 to 3 week survival (0-3WKS), 0 to 12 week survival (0-12WKS), 0 to 24 week survival (0-24WKS), 2 to 3 week survival (2-3WKS), 4 to 12 week survival (4-12WKS) and 13 to 24 week survival (13-24WKS) of ostrich chicks recorded during the 2000 to 2008 breeding seasons.

Trait	Model 1	Model 2	Model 3	Model 4	Model 5
0-1WKS	9082.41 (0.057)	9109.46 (0.054)	9114.75 (0.055)	9115.97 (0.056)	9116.59 (0.056)
0-3WKS	4073.46 (0.151)	4128.75 (0.141)	4129.66 (0.142)	4128.89 (0.142)	4129.66 (0.142)
0-12WKS	3235.53 (0.179)	3314.33 (0.166)	3316.19 (0.169)	3314.78 (0.168)	3316.19 (0.169)
0-24WKS	4022.56 (0.153)	4090.35 (0.144)	4091.25 (0.145)	4090.75 (0.145)	4091.26 (0.145)
2-3WKS	4767.03 (0.124)	4810.07 (0.116)	4810.07 (0.116)	4810.07 (0.116)	4810.07 (0.116)
4-12WKS	1937.37 (0.186)	1990.15 (0.171)	1992.08 (0.174)	1990.85 (0.173)	1992.08 (0.174)
13-24WKS	1629.49 (0.153)	1637.31 (0.147)	1637.44 (0.147)	1637.31 (0.147)	1637.44 (0.148)

*The model of choice is depicted in bold

Model 1: $y_{ij} = X\beta + e_{ikj}$

Model 2: $y_{ij} = X\beta + Z_1a_i + e_{ikj}$

Model 3: $y_{ij} = X\beta + Z_1a_i + Z_3pe_j + e_{ikj}$

Model 4: $y_{ij} = X\beta + Z_1a_i + Z_2m_j + e_{ikj}$

Model 5: $y_{ij} = X\beta + Z_1a_i + Z_2m_j + Z_3pe_j + e_{ikj}$

Table 4.2 Estimates for direct heritability (h^2), the maternal genetic effect (m^2), the dam permanent environmental effect (c^2) and the phenotypic variance (σ_p^2) of 0 to 1 week survival (0-1WKS), 0 to 3 week survival (0-3WKS), 0 to 12 week survival (0-12WKS), 0 to 24 week survival (0-24WKS), 2 to 3 week survival (2-3WKS), 4 to 12 week survival (4-12WKS) and 13 to 24 week survival (13-24WKS) for ostrich chicks recorded during the 2000-2008 breeding season.

Trait	h^2	m^2	c^2	σ_p^2
0-1WKS	0.01 ± 0.01	0.03 ± 0.01	-	0.13
0-3WKS	0.08 ± 0.01	-	-	0.15
0-12WKS	0.05 ± 0.02	-	-	0.18
0-24WKS	0.06 ± 0.01	-	-	0.15
2-3WKS	0.07 ± 0.01	-	-	0.062
4-12WKS	0.05 ± 0.02	-	0.02 ± 0.01	0.19
13-24WKS	0.04 ± 0.016	-	-	0.15

* h^2 is the additive genetic effect, m^2 is the maternal genetic effect and c^2 is the dam permanent environmental effect

Dam permanent environment effects influenced 4-12WKS, but the applicable variance ratio was very small in magnitude (0.02). The explanation of this effect is not straightforward. It could be argued that it is due to residual maternal investment in the eggs the chicks hatched from, as the chicks were reared artificially in the complete absence of parental care. Nevertheless the variance components barely reached significance, and could alternatively be artefacts from biological processes which are poorly understood at present.

Multi-trait analyses

The three-trait analyses attained heritability estimates that were in close correspondence with those derived from single-trait analyses for the respective survival traits (Table 4.3). The average moisture loss up to 35 days of incubation (ML35) was 12.84% and ranged from 6.18 to 30.50%. These results are in accordance with previous literature findings (Brown *et al.*, 1996; Brand *et al.*, 2008a; 2009). Estimates of the additive genetic component ranged between 0.34 and 0.44 which were similar to those attained by Brand *et al.*, (2008a) ($h^2 = 0.40 \pm 0.13$), although higher than that of Brand *et al.*, 2009 (0.26 ± 0.06) despite similar standard errors. The estimate of the dam permanent environmental variance ratio ($c^2 = 0.289 \pm 0.03$) were also consistent with that attained by Brand *et al.* (2009; 0.30 ± 0.04).

Table 4.3 Estimates of direct heritability (h^2), the maternal genetic effect (m^2) and the dam permanent environmental effect (c^2) from three-trait analyses for moisture loss at 35 days incubation (ML35), day of pip (PD), day old chick weight (DOCW), 0 to 12 week survival (0-12WKS), 0 to 3 week survival (0-3WKS) and 0 to 1 week survival (0-1WKS).

Trait	h^2	m^2	c^2
ML35	0.41 ± 0.06	-	0.24 ± 0.03
PD	0.09 ± 0.03	-	0.05 ± 0.01
DOCW	0.32 ± 0.05	0.42 ± 0.03	-
0-1WKS	0.02 ± 0.01	0.03 ± 0.01	-
0-3WKS	0.07 ± 0.01	-	-
0-12WKS	0.04 ± 0.02	-	-

The day-old chick weight (DOCW) in this analysis ranged from 487 to 1226g with an average weight of 853.43g. This mean corresponds well to other findings on the same resource flock (Cloete *et al.*, 2001; Bunter & Cloete, 2004; Brand *et al.*, 2008). Day-old chick weight generally ranges from 780 to 975g (Verwoerd *et al.*, 1999), although larger ranges from 464 to 1300g have been reported (More, 1996). The additive genetic parameter estimates were moderate ($h^2 = 0.32$ to 0.39) and resembled those published by Brand *et al.* (2009). At 0.42 to 0.47 , the maternal genetic component was however higher than those derived in previous studies. For both parameter estimates, low standard errors were achieved.

Table 4.4 Estimates (\pm s.e.) of genetic (r_g), environmental (r_e) and phenotypic (r_p) correlations between moisture loss at 35 days incubation (ML35), day of pip (PD) and day old chick weight (DOCW) and cumulative age specific survival traits: 0 to 1 week survival (0-1WKS), 0 to 3 week survival (0-3WKS), 0 to 12 week survival (0-12WKS).

Trait	Correlated trait	r_g	r_e	r_p
ML35	0-1WKS	0.231 ± 0.145	-0.034 ± 0.025	0.014 ± 0.012
	0-3WKS	0.151 ± 0.133	-0.052 ± 0.024	-0.009 ± 0.013
	0-12WKS	0.072 ± 0.187	-0.036 ± 0.025	0.006 ± 0.014
DOCW	0-1WKS	0.379 ± 0.272	0.084 ± 0.026	0.065 ± 0.015
	0-3WKS	0.182 ± 0.133	0.084 ± 0.028	0.073 ± 0.012
	0-12WKS	0.218 ± 0.153	0.058 ± 0.027	0.061 ± 0.012
PD	0-1WKS	-0.056 ± 0.172	-0.039 ± 0.013	-0.046 ± 0.011
	0-3WKS	0.069 ± 0.164	-0.106 ± 0.013	-0.090 ± 0.011
	0-12WKS	-0.024 ± 0.264	-0.049 ± 0.014	-0.053 ± 0.011

The day of external pipping (PD) ranged from 35.7 days to 46.3 days with a mean of 41.92 days. This mean falls between the 41.3 days and 42 days reported by Cloete *et al.* (2001) and Brand *et al.* (2009) respectively. The low heritability estimates attained in the respective three-trait analyses were almost half those estimated by Brand *et al.* (2008). Dam permanent environment effects were also low, but closely resembled previous findings (Brand *et al.*, 2008).

ML35 and DOCW exhibited a moderate negative genetic correlation which accorded with the residual and phenotypic correlations as far as sign is considered ($r_g = -0.517 \pm 0.08$; $r_e = -0.39 \pm 0.07$; $r_p = -0.31 \pm 0.01$). This is not unexpected, as eggs with high levels of water loss would lead to dehydrated chicks, with a lower day-old weight and vice versa. In essence, PD and ML35 were uncorrelated ($r_g = -0.044 \pm 0.184$; $r_e = 0.207 \pm 0.121$; $r_e = -0.002 \pm 0.032$; $r_p = 0.016 \pm 0.018$). DOCW was lowly correlated with PD on the genetic level ($r_g = 0.218 \pm 0.153$; $r_e = -0.064 \pm 0.036$; $r_p = 0.007 \pm 0.015$). The direction and magnitude of these correlations concurs with those previously reported by Brand *et al.* (2009).

The genetic correlations of ML35 with cumulative survival over different time intervals were generally positive and tended to decline as the time interval increased (Table 4.4). However, none of these correlations reached a level of double the corresponding standard error. The quality of hatched chicks is affected by moisture loss of the egg (Adewumi *et al.*, 2008). Cloete *et al.* (2001) found that mortalities to 28 days of age increased with elevated ML35, while Blood *et al.* (1998) reports embryonic survival to have a curvilinear relationship with the moisture loss of the egg during incubation. This non-linear relationship may also be appropriate for early chick survival, hence explaining the discrepancy between our findings of a lowly positive correlation and that of Cloete *et al.* (2001). It is reasonable to assume that the survival of oedemateous chicks hatching from low moisture loss eggs, as well as dehydrated chicks hatching from high moisture loss eggs may be compromised relative to chicks hatching from eggs with intermediate levels of water loss. The genetic correlations of day of external pipping and age specific survival traits were low and variable in sign. Both ML35 and PD exhibited negative environmental or residual correlations with cumulative survival traits. An environment promoting excessive moisture loss or a propensity towards a delay in external pipping will therefore be less conducive for survival. These correlations mostly reach a level of double the corresponding standard error, but were mostly below 0.1 in magnitude.

Day-old chick weight demonstrated the most consistent relationships with survival, with a low to moderate positive genetic correlation (Table 4.4). The direction of these correlations are consistent with the findings of Cloete *et al.* (2001) and Bonato (2009) who demonstrated that day-old chick

weight was positively related to early survival of ostrich chicks. It has been proposed that heavier chicks may possess a larger anatomical structure with a superior nutritional supplementation and elevated growth rate, all of which promote survival (Parsons, 1970; Galbraith, 1988; Reid & Boersma, 1990; Bolton, 1991; Perrins 1996). The positive environmental correlation between DOCW and respective survival demonstrates an environment conducive to producing heavier chicks is therefore also favourable for survival. The maternal correlation between 0-1WKS and DOCW was negative in sign, very low and close to zero, with a large standard error ($r_m = -0.019 \pm 0.135$).

Conclusion

Ostrich chick survival to 24 weeks of age exhibited genetic variation, albeit at fairly low levels. Early post hatching survival (0 to 1 weeks) was maternally influenced while from 4 to 12 weeks post hatch was affected by the dam permanent environment. Heavier chicks were more likely to survive to 3 weeks post hatch and an environment conducive to producing larger chicks endorses survival. Further studies are required to ascertain how this genetic variation and the genetic correlations can be exploited to ensure that chick survival in the industry is enhanced.

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Chapter 5

Genetic parameters for chick survival to 6 months post hatch in South African Black ostriches (*Struthio camelus* var. *domesticus*) using a threshold-linear model and employing Gibbs sampling

Abstract

Data of ostrich chicks were used to estimate genetic parameters for age-specific survival from 0 to 24 weeks, 0 to 3 weeks, 0 to 1 weeks, 2 to 3 weeks and 13 to 24 weeks. Respective correlations of survival traits with incubation moisture loss to 35 days incubation, day of external pipping and day-old chick weight were also determined. Data of up to 10418 chick records from a commercial pair bred ostrich flock in Oudsthoorn, South Africa was assessed by Bayesian inference, using Gibbs sampling. Additive genetic estimates for all survival traits were low to moderate at respectively, 0.06 for 0 to 24 weeks, 0.08 for 0 to 3 weeks, 0.12 for 0 to 1 week, 0.08 for 2 to 3 weeks and 0.10 for 13 to 24 weeks. Maternal variances for survival traits were also low. Early survival exhibited a moderate favourable relationship with day old chick weight on the additive genetic level. Further research is required to determine how the significant additive genetic variation may be exploited to improve chick survival.

Introduction

The importance of determining variance and (co)variance components for survival has been illustrated in Chapter 4. Gionola & Fernando (1986) originally proposed the Bayesian approach as an alternative method of estimating variance components in traits not necessarily conforming to a normal distribution. In 1990, Gianola & Foulley (1990) developed a new approach to Bayesian Inference utilizing integrated likelihoods. The Gibbs sampler was then introduced as a Markov Chain Monte Carlo numerical integration method that permits inferences about joint or marginal distributions (Geman & Geman, 1984; Wang et al., 1993). Gibbs sampling enables the derivation of Bayesian posterior distributions that are computationally awkward as a result of the numerical assimilation necessitated to obtain such distributions (Van Tassel & Van Vleck, 1996). The Gibbs sampling algorithm is employed by utilizing a fully conditional distribution of an unknown parameter with all other parameters in the model and data that are recognized, to generate a realized value for each unknown variable in a model (Van Tassel & Van Vleck, 1996). This cycle is repeated until it eventually converges to the posterior distribution from which values are extracted and termed

random samples from the posterior distribution (Van Tassel & Van Vleck, 1996). The number of repeats discarded prior to values being considered as samples is commonly termed the “burn-in period” (Van Tassel & Van Vleck, 1996). In Bayesian estimations everything in a model is assumed to be random including variances estimated which tend towards Chi-squared distributions under an animal model. Fixed effects are assumed to have uniform distributions. Animal genetic effects and residual effects are also usually assumed to have normal distributions under an animal model.

As demonstrated in Chapter 4, the determination of variance components at later ages may be censored and may provide inadequate information to determine reliable inferences about (co)variance components (Wang *et al.*, 1993). This is a common problem in animal breeding (Lin & Berger, 2001). Restricted Maximum Likelihood acquires additional information through the incorporation of related animals to the database when estimating (co)variance components (Lin & Berger, 2001). Gibbs sampling, however, provides a supplementary option by combining prior knowledge with current information such that those animals with unknown (died at younger ages) parameters (variance components and fixed effects) are assigned priors and can therefore be included in the analyses (Gwaze & Woolliams, 2001; Lin & Berger, 2001). This method permits inferences to be made regarding joint or marginal distributions of the parameters of interest, unlike REML methods which only allow for joint distributions (Gwaze & Woolliams, 2001). Binomial traits with extreme frequencies, and therefore distinctly skewed distributions will, therefore also benefit from threshold linear modelling that employs Gibbs sampling.

The aim of this chapter was therefore to determine variance and (co)variance parameters via multi-trait analyses utilizing Gibbs sampling for age specific survival traits to 24 weeks post-hatch.

Materials and Methods

Description of the data

A commercial pair-bred ostrich flock maintained at the Oudtshoorn Research Farm, South Africa formed the base population, providing the pedigree and performance data for the present study. South African Black ostrich (*Struthio camelus* var. *domesticus*) data recorded from 2000 to 2008 were used. The pedigree file involved 13073 individuals over 6 generations that were the progeny of 387 sires and 378 dams. The management of the breeding pairs and the eggs has previously been discussed in Chapter 3 as well as in the literature (Bunter & Cloete, 2004; Brand *et al.*, 2007; Cloete *et al.*, 2008).

Traits Recorded

The definitions of age specific survival traits have been discussed in Chapter 3. The following traits were analysed (See Table 3.1):

- 0 to 1 week survival (0-1WKS), comprising of 10418 records
- 0 to 3 week survival (0-3WKS), comprising of 10418 records
- 0 to 24 week survival (0-24WKS), comprising of 10418 records
- 2 to 3 week survival (2-3WKS), comprising of 9729 records, only including those chicks that were alive at 2 weeks post hatch
- 13 to 24 week survival (13-24WKS), comprising of 3886 records, only including those chicks that were alive at 13 weeks post hatch
- Moisture loss at 35 days incubation (ML35)
- Day of external pipping (PKDAY)
- Day old chick weight (DOCW)

Statistical Analyses

Five four-trait linear threshold analyses were fitted to the dataset with incubation moisture loss at 35 days of incubation (ML35), day of pipping (PD) and day-old chick weight (DOCW) together with either 0 to 24 week survival (0-24WKS), 0 to 3 week survival (0-3WKS), 0 to 1 week survival (0-1WKS), 2 to 3 week survival (2-3WKS) or 13 to 24 week survival (13-24WKS) as the dependent variables. Survival traits were treated as binary traits with 1 identifying those chicks that died and 0 representing the chicks that survived while ML35, PD and DOCW were considered as continuous variables. The transformation was required as traits with zero values are set to missing by default.

The following equation for each four-trait model was fitted to the dataset:

$$Y_{ijkqr} = B_{ik} + O_{ij} + D_{iq} + P_{ir} + a_{im} + e_{ijkqr mn}$$

Where:

Y_{ijkqr} is the vector of observations for the respective traits

i is indicative of the respective traits ($i = 4$)

B_{ik} is fixed effect k for the i^{th} trait

O_{ij} is fixed effect j for the i^{th} trait

D_{iq} is fixed effect q for the i^{th} trait

P_{ir} is fixed effect r for the i^{th} trait

a_{im} is the additive genetic effect of the n^{th} animal for the i^{th} trait

$e_{ijkqr mn}$ is the vector of randomly distributed residual effects

THRGIBBS1F90 software was used to estimate variance components and genetic parameters in threshold-linear mixed animal models (Misztal *et al.*, 2002; Mizstal, 2008). This software package enables the estimation of any combination of continuous categorical traits. POSTGIBBSF90 software was used to perform the Post Gibbs analysis (Misztal *et al.*, 2002). Genetic and environmental (co)variance parameters were estimated and genetic parameters for the respective traits were thus derived.

A chain of 300 000 samples were run in all models with the first 50000 cycles used as the burn-in period. Every 10th subsequent sample was used to compute parameters, posterior standard deviations (PSDs) and 95% confidence intervals. Direct genetic and residual (environmental) correlations were computed from these analyses. The analyses suggested that additive animal, maternal genetic and dam permanent environmental variance ratios were all generally significant in all analyses (posterior standard deviation < 50% of the corresponding variance component). All these effects were thus included in the final analyses.

Results and Discussion

Additive genetic parameter estimates for day of external pipping and day-old chick weight did not differ greatly from those obtained via three-trait analyses in Chapter 4 (Table 4.5). Day-old chick weight was affected by an equally large maternal component. The distribution of variation for incubation moisture loss to 35 days incubation was, however notably different from that obtained in ASREML three-trait analyses. Both the additive genetic and dam permanent environmental variations were reduced from 0.41 to 0.31 and 0.24 to 0.08 respectively, with a subsequent addition of a moderate maternal component.

Cumulative survival to 3 weeks and to 24 weeks as well as 2 to 3 weeks survival exhibited additive genetic components similar to those obtained using linear models. Survival during the first week as well as survival from 13 to 24 weeks however demonstrated a notable increase in the additive genetic and maternal variation when analysed with the more appropriate approach, using Gibbs sampling (0-1WKS: $h^2 = 0.01$ to 0.12 and $m^2 = 0.03$ to 0.08 ; 13-24WKS: $h^2 = 0.04$ to 0.10 and $m^2 = 0$ to 0.07). Mean survival during the first week post hatch was high at 0.93, and may subsequently represent a more skewed distribution that is better accommodated by Bayesian inference, using Gibbs sampling. Age specific survival from 13 to 24 weeks was severely censored. Gibbs sampling was therefore a more suitable method for the determination of variance components.

The relatively large fullsib family structure of ostriches can possibly be used to identify lines with an inherently better survival. When the marked breed difference in survival between SA Black and Zimbabwean Blue chicks (Engelbrecht *et al.*, 2008) is considered, it can be assumed that there is a genetic basis to this survival, waiting to be exploited.

Table 5.1 Estimates of direct heritability (h^2), the maternal genetic effect (m^2) and the dam permanent environmental effect (c^2) from five respective four-trait linear-threshold analyses, involving moisture loss at 35 days of incubation (ML35), day of pipping (PD) and day-old chick weight (DOCW) when analysed together with either 0 to 24 week survival (0-24WKS), 0 to 3 week survival (0-3WKS), 0 to 1 week survival (0-1WKS), 2 to 3 week survival (2-3WKS) or 13 to 24 week survival (13-24WKS) of ostrich chicks recorded during the 2000 to 2008 breeding seasons.

Trait	h^2	m^2	c^2
ML35	0.31 ± 0.05	0.25 ± 0.05	0.08 ± 0.04
PD	0.10 ± 0.03	0.05 ± 0.01	0.02 ± 0.01
DOCW	0.33 ± 0.05	0.40 ± 0.06	0.05 ± 0.03
0-1WKS	0.12 ± 0.04	0.08 ± 0.02	0.03 ± 0.01
0-3WKS	0.08 ± 0.02	0.04 ± 0.01	0.02 ± 0.01
0-24WKS	0.06 ± 0.02	0.05 ± 0.01	0.02 ± 0.01
2-3WKS	0.08 ± 0.03	0.05 ± 0.01	0.02 ± 0.01
13-24WKS	0.10 ± 0.04	0.07 ± 0.02	0.03 ± 0.02

Additive and maternal correlations between age-specific survival traits and moisture loss at 35 days incubation were comparatively low with standard errors typically double the corresponding covariance ratios (Table 5.1). Dam permanent environmental correlations between moisture loss and all age specific survival traits except 13-24WKS, were quite high, although corresponding standard errors were equally high. The dam permanent environmental variances for these traits are however comparatively small which, together with the high standard errors, demonstrate these dam permanent environmental correlations to be essentially inaccurate.

Genetic correlations of interval-specific survival with day-old chick weight were positive in sign (the only exception being with 13-24 week survival), low to moderate in magnitude, and larger than the corresponding standard errors (Table 5.2). Although this cannot be considered as compelling evidence of a positive genetic correlation of survival with chick weight, it should be noted that heavier chicks were also more likely to survive than lighter contemporaries in the studies of Cloete *et al.* (2001) and Bonato (2009). It has been proposed that heavier chicks may possess a larger anatomical structure with a superior yolk sac supplementation and elevated growth rate, all of

which promote survival (Parsons, 1970; Galbraith, 1988; Reid & Boersma, 1990; Bolton, 1991; Perrins 1996). However, this result should be treated with caution. It is well known that chicks are often graded on day-old weight, with heavier chicks being preferred (Fasenko *et al.*, 2009). However, the standardization of egg size (and thus day-old chick weight; $r_g > 0.90$; Bunter & Cloete, 2004) to an intermediate optimum has been propagated as a solution to the relatively low and variable incubation success of ostrich eggs (Deeming *et al.*, 1993; Deeming, 1995; Brown *et al.*, 1996; More, 1996; Van Schalkwyk *et al.*, 1996).

Table 5.2 Estimates (\pm s.e.) of genetic (r_g), maternal (r_m) dam permanent environmental (r_{pe}) and environmental (r_e) correlations from five respective four-trait linear-threshold analyses, involving moisture loss at 35 days of incubation (ML35), day of pipping (PD) and day-old chick weight (DOCW) when analysed together with either 0 to 24 week survival (0-24WKS), 0 to 3 week survival (0-3WKS), 0 to 1 week survival (0-1WKS), 2 to 3 week survival (2-3WKS) or 13 to 24 week survival (13-24WKS) of ostrich chicks recorded during the 2000 to 2008 breeding seasons.

Trait	Correlated trait	r_g	r_m	r_{pe}	r_e
ML35	PD	0.02 ± 0.15	0.21 ± 0.16	-0.04 ± 0.32	-0.02 ± 0.03
	DOCW	-0.37 ± 0.12	-0.57 ± 0.14	-0.41 ± 0.34	-0.50 ± 0.08
	0-1WKS	0.19 ± 0.22	-0.03 ± 0.19	0.54 ± 0.47	-0.04 ± 0.05
	0-3WKS	0.15 ± 0.20	0.08 ± 0.21	0.55 ± 0.41	-0.06 ± 0.03
	0-24WKS	0.15 ± 0.22	0.14 ± 0.22	0.30 ± 0.59	-0.06 ± 0.03
	2-3WKS	0.04 ± 0.22	0.12 ± 0.18	0.43 ± 0.35	-0.06 ± 0.04
	13-24WKS	-0.05 ± 0.25	0.17 ± 0.20	-0.15 ± 0.40	-0.04 ± 0.05
DOCW	PD	0.08 ± 0.15	-0.01 ± 0.16	0.39 ± 0.36	-0.05 ± 0.04
	0-1WKS	0.24 ± 0.21	0.03 ± 0.20	-0.15 ± 0.60	0.15 ± 0.06
	0-3WKS	0.24 ± 0.19	0.11 ± 0.20	-0.18 ± 0.45	0.13 ± 0.04
	0-24WKS	0.16 ± 0.20	0.04 ± 0.20	0.11 ± 0.61	0.06 ± 0.04
	2-3WKS	0.21 ± 0.19	0.10 ± 0.17	0.03 ± 0.38	0.09 ± 0.04
	13-24WKS	-0.07 ± 0.26	-0.05 ± 0.20	0.10 ± 0.45	-0.04 ± 0.07
PD	0-1WKS	-0.10 ± 0.24	-0.09 ± 0.19	-0.01 ± 0.36	-0.09 ± 0.03
	0-3WKS	0.06 ± 0.22	-0.04 ± 0.20	-0.12 ± 0.35	-0.15 ± 0.02
	0-24WKS	-0.14 ± 0.23	0.04 ± 0.19	-0.19 ± 0.36	-0.02 ± 0.02
	2-3WKS	0.09 ± 0.22	-0.04 ± 0.21	-0.01 ± 0.32	-0.15 ± 0.02
	13-24WKS	-0.07 ± 0.26	0.04 ± 0.21	0.06 ± 0.38	0.08 ± 0.03

The positive environmental correlation between DOCW and respective survival traits demonstrates that an environment conducive to producing heavier chicks is also favourable for survival. The maternal correlations of 0-3WKS survival and 2-3WKS survival with DOCW were low, and amounted to about half the corresponding standard error ($r_m = 0.11 \pm 0.20$ and 0.10 ± 0.17 respectively). Dam permanent environment correlations with survival range from low to moderate, with negative correlations demonstrated for early survival (0-1WKS and 0-3WKS). High standard errors were, however, also computed in this case.

Interval-specific chick survival was largely unrelated to pipping time at all levels of the individual chicks. It should be noted, however, that the environmental correlations of early chick survival (to 3 weeks) were generally negative. These results infer that chicks pipping at a later stage of incubation were less likely to survive the initial period after hatching. When the incubation period extends appreciably beyond 42 days, chicks can be assisted to hatch (Brand *et al.*, 2009). Literature results suggest that ostrich chicks assisted to hatch have a reduced survival (25%) and extremely poor early growth (Deeming & Ayres, 1994; Ipek & Sahan, 2004).

Conclusion

Selection for early chick survival as well as survival from 13 to 24 weeks post-hatch may prove beneficial, when breeding values estimated on the underlying liability scale are used. Linear-threshold modelling utilizing Gibbs sampling exhibits more realistic parameter estimates for early and late chick survival where data is more non-normally distributed or severely censored. Selection for heavier chicks may result in an improved chick survival rate. However, detailed methods for such selection strategy needs to be deliberated, as only survivors can be considered for selection, and the overall number of chicks surviving to 24 weeks of age are discouragingly low. Further research is needed to identify an appropriate strategy for the genetic improvement of ostrich chick survival.

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Chapter 6

The effect of rearing method on ostrich chick survival and chick weight: Foster parenting, human imprinting and conventional handling

Abstract

The effect of human imprinting or regular human care and foster parenting by adult ostriches on the survival and growth performance of ostrich chicks were investigated in two separate experiments. In the first experiment, growth rate and survival of chicks imprinted on humans was compared to that of chicks reared by adult foster parents ($n = 100$ for each group). Treatment did not affect chick survival to 3 weeks (0.90 for imprinted chicks vs. 0.89 for foster chicks), nor from 4 to 12 weeks (0.86 vs. 0.83 respectively). Chick weight was not significantly different between groups at 4 weeks of age but at older ages, those chicks reared by foster parents consistently outperformed imprinted chicks (means \pm SE's being 12.8 ± 0.4 vs. 8.2 ± 0.4 kg at 9 weeks, 37.1 ± 0.8 vs. 19.9 ± 0.80 kg at 18 weeks and 46.2 ± 1.1 vs. 28.6 ± 1.2 kg at 22 weeks). Treatments in the second experiment comprised of a human-imprinted group of chicks and a group subjected to conventional rearing methods. The latter treatment corresponded to conventional chick rearing practices as used at the research location. Chick survival was significantly higher for imprinted chicks than for conventionally reared chicks (0.97 vs. 0.84), although chick weight was independent of treatment at 4 weeks (6.27 ± 0.16 kg for the imprinted group vs. 6.18 ± 0.17 kg for the conventional group) and at 15 weeks (respectively 16.5 ± 0.68 vs. 15.2 ± 0.70 kg). Overall, chicks reared by foster parents were heavier than human-imprinted chicks, while early survival of imprinted chicks was better than that of chicks reared by conventional handling. Imprinting thus affected survival of ostrich chicks relative to conventional rearing practices. Because most ostrich chicks are reared using conventional methods, the present study indicates that improvements can be made by adopting alternative approaches. Further studies are needed to ascertain how either foster parenting or imprinting may be utilized to enhance chick performance, including the study of long-term consequences of these practices.

Introduction

Considerable progress on human-animal interactions in agriculture has been achieved recently as a consequence of growing concerns about farmed animal welfare (Rushen *et al.*, 1999; Zulkifli & Azah, 2004). Habituation to human handling and environmental enrichment during rearing are two methods that may reduce the overall stress levels of farm animals, with positive effects on their behaviour, productivity and welfare (Mills & Faure, 1990; Jones & Waddington, 1992; Hemsworth *et al.*, 1993; Reed *et al.*, 1993; Rushen *et al.*, 1999). Environmental enrichment is a vague concept referring to improvements to the environment of captive animals (Newberry, 1995). The imprinting phenomenon is potentially a method of environmental enrichment (Savaterra *et al.*, 1994).

In avian species, recent hatchlings form an attachment with any individual present at the time of hatching (Matsushima *et al.*, 2003; Slagsvold & Hansen, 2008). This attachment, often irreversible, is termed filial imprinting and accounts for a number of fundamental animal behaviours and social preferences (Slagsvold & Hansen, 2008). Environmental enrichment and regular handling has been shown to improve growth, reproductive performance, egg production, feed conversion rate, antibody production, disease resistance, survival and general behaviour in chickens (Jones *et al.*, 1980; Jones & Hughes, 1981; Collins & Siegel, 1987; Gvoryahu *et al.*, 1989; Jones & Waddington, 1992; 1993; Barnett *et al.*, 1994; Hemsworth *et al.*, 1994). It may thus, potentially, have profound effects on the way farm animals are handled.

Foster parenting, on the other hand, may also promote the welfare, survival and performance of ratite chicks (Barri *et al.*, 2005; Janse van Vuuren, 2008). Ostrich chicks reared by breeding pairs exhibit superior survival compared to that of chicks reared by using conventional intensive methods (Janse van Vuuren, 2008). Allowing chicks to be reared by foster parents, has the effect that chicks exhibit reduced stress levels, and breeder pairs are provided with the opportunity to express natural parental care (Janse van Vuuren, 2008; Cloete & Malecki, 2011). The environment of both the chicks and the breeding pairs may thereby be enriched. Rabbits have also been reported to effectively supplement the mother figure and improve the welfare of the chicks (Madeiros, 1997). Consumption of the rabbit dung by the ostrich chicks provides the chicks with vitamins B and K while also inoculating the ostrich chicks intestines with beneficial bacteria, preventing yolk sac problems and other diseases associated with poor colonisation of the gut (Madeiros, 1997). The adoption approach necessitates less effort and investment than the rearing of chicks in special facilities, while also preventing the imprinting of chicks on humans (Bubier *et al.*, 1998; Labaque *et al.*, 1999).

However, imprinting is seen as problematic in commercially farmed ostriches, as the imprinted bird may subsequently direct its sexual attention to those humans on which it was imprinted (Bubier *et al.*, 1998). In contrast, imprinting on humans may play an important role in efforts to devise a viable protocol for assisted reproduction (AR) in this species (Malecki & Rybnik-Traskowska, 2011). Artificial insemination resulting from research on AR would lead to improved industry data for analysis by allowing the accurate partitioning of random effects (Cloete *et al.*, 2008) and would also reduce the number of males required in industry flocks, leading to an obvious reduction in feeding costs.

Environmental enrichment/imprinting/foster parenting and regular handling are powerful tools and their independent or integrated application may alleviate stress, thereby satisfying many of the limitations imposed by related behaviour (Jones & Waddington, 1993). The potential alleviation of stress in ostriches through regular human handling and/or environmental enrichment techniques is therefore an important objective in animal welfare and production (Jones & Waddington, 1993). Foster parenting, on the other hand, provides a low-cost alternative for the rearing of ratite chicks. This practice has direct advantages in terms of growth of greater rhea chicks (Barri *et al.*, 2005) and the survival of ostrich chicks (Janse van Vuuren, 2008), possibly reflecting an alleviation in the stress experienced by the young chick as a result of the presence of foster parents.

Against this background, a preliminary study was conducted to investigate whether imprinting on humans (as a potential form of environmental enrichment) and regular handling can improve the survival and growth of ostrich chicks. The effectiveness of the practice of foster-parenting was assessed simultaneously as a low-cost alternative rearing method.

Materials and methods

Day-old chicks were obtained from the pair-bred ostrich flock at the Oudtshoorn Research Farm. The management of the breeding pairs and the eggs in this flock has been previously described (Bunter & Cloete, 2004; Cloete *et al.*, 2008). Two experiments were performed.

Experiment 1: A total of 200 ostrich chicks, hatched over a period of 4 days, were randomly assigned to two groups. The first group comprised of chicks raised by breeder pairs as foster-parents in an extensive rearing environment with minimal human contact to prevent imprinting onto humans (Bubier *et al.*, 1998). Three breeder pairs (referred to as pairs 21, 23 and 29) were selected on previous knowledge of their foster parenting ability from the breeder pairs maintained on the Oudtshoorn Experimental Farm. The ages of the male (M) and female (F) of each

respective pair were M21: 9 years, F21: 13 years, M23: 18 years, F23: 17 years, M29: 11 years and F29: 10 years. The selected breeder pairs incubated and hatched at least one of their own eggs. The experimental eggs ($n = 100$ divided 33:33:34) were incubated in the hatchery in synchronization with those eggs incubated naturally by the breeder birds, i.e. to ensure that all eggs hatched at the same time. After hatching, chicks from the artificially incubated eggs were added to those of the breeder birds (Figure 6.1) (Labaque *et al.*, 1999). Each foster parent pair, together with their respective chicks, were maintained in 1-2 ha lucerne camps with water and feed available *ad libitum*.



Figure 6.1 Adult foster parent ostrich pair with their respective group of chicks.

The second group, the human imprinting group, consisting of 100 chicks, were reared using conventional chick-rearing practices (Bunter & Cloete, 2004) in an intensive rearing facility with food and water *ad libitum* and artificial heating by means of overhead long-wave infrared heaters. Upon hatching, chicks remained in the hatchery as per standard farm practice and for 30 days were given human contact (Figure 6.2) according to the following schedule: From hatching to 10 days of age, human presence was established for a 100% of daylight hours (5h45-18h30). The chicks were familiarized with touch, voice, hand feeding and a general human presence. The person who remained with them wore a white laboratory overcoat at all time. The degree to which ostriches distinguish individuals has not as yet been fully ascertained, although it has been suggested that in livestock, habituation to the original handler is rapidly generalized to similarly dressed, but otherwise unfamiliar humans (Hemsworth *et al.*, 1996). After 10 days, the human presence was decreased to 50% of daylight hours (6h00-7h00; 9h00-10h00; 11h00-12h00; 13h00-14h00; 15h00-16h00; 17h00-18h00) for another 10 days. From day 21 to day 30 a human remained with the chicks from 7h00 to 8h00 and then a human was present for 30 minutes every 1.5 hours until 17h00, followed by a full hour from 17h00 to 18h00. At 10 days post hatch the chicks were split into 3 groups placed into adjacent pens. Chicks were weighed at hatching and again at 4, 9, 18 and 22 weeks of age. In addition, all mortalities were recorded for both treatment groups.

The fostered birds were accommodated outside with access to lucerne pasture as well as standard balanced rations, whereas the imprinted chicks only had the same standard balanced ration (Cooper, 2004) as a food source. When the imprinted chicks were placed outside at 12 weeks, they had access to the same food sources supplied to the foster parented chicks (a balanced diet and lucerne pasture).



Figure 6.2 Human subject with the newly hatched ostrich chicks in the hatchery.

Experiment 2: A group of day-old chicks were divided into two groups. One group (control), comprising of 97 chicks, were distributed between two adjacent pens and exposed to the standard intensive rearing protocol of the Oudtshoorn Experimental Farm (Bunter, 2002; Bunter & Cloete, 2004). The other group (treatment) encompassed the 'imprinting, human foster group' that were raised in identical separate rooms distributed between two adjacent pens, with the addition of a regular human presence. The chicks used hatched over a period of 3 days. From day 1-5 a person remained with the chicks from 6h00 to 18h00. Thereafter, the time spent with the chicks decreased by 3 hours every 5 days. The hours spent with the human subject were evenly spread according to three pivot times (8h00, 12h00 and 16h00). Chicks were familiarized with human speech, touch, movement, hand feeding along with a general human presence (Figure 6.3). The human would sit on a chair placed within each of the two adjacent pens, would sit on a cushion on the floor or walk around the pen. All mortalities were recorded. The regular human handling phase of the trial concluded at day 21. Thereafter all experimental chicks were combined and exposed to the same standard chick-rearing protocol. Weighing took place at hatching and at 4 and 9 weeks of age.



Figure 6.3 Ostrich chicks exposed to regular human contact.

Individual chicks were used as experimental units in both experiments. It is conceded that groups of chicks treated as experimental units would be a better way of approaching the problem. However, the limited facilities available for the group sizes required for such an experiment, the number of indoor pens available, as well as the number of foster-parents required, would have made experiments with such a design impossible. Moreover, the research was designed as a preliminary study to explore potential benefits associated with the alternative management options. It could be argued that the comparison of individual chicks would be appropriate, especially in Experiment 2, as all facilities were similar, with the exception of human imprinting. It was also possible to combine these chicks soon after the cessation of the imprinting period. A more definite difference was present in Experiment 1, where the chicks could only be combined after recording for this experiment ceased.

Using data of individual chicks, Chi-square analyses were used to compare treatment effects upon age-specific chick survival. The effect of different treatments on age-specific weights was ascertained by using standard one-way ANOVA procedures. A supplementary analysis comparing the survival and performance of the chicks raised by the three separate breeding pairs used for fostering was accordingly done via Chi-square analysis and one-way ANOVA.

Results and discussion

In Experiment 1, there was no difference in chick survival to 12 weeks or chick weight at 4 weeks of age between fostered chicks and the imprinted chicks. However, as the chicks got older, the foster-reared chicks outperformed the imprinted chicks, having heavier weights and improved survivability from 13 to 24 weeks post hatch (Table 5.1). Relative to the imprinted group, the mean weights of the foster-parented group were improved by 4.6kgs at 9 weeks, by 17.2kgs at 18 weeks, and by 20.6kgs at 22 weeks. These results are comparable to that of Barri *et al.*, (2005) who

reported no difference in survival rates of adopted Greater Rhea chicks compared to those reared intensively. They also proposed adoption to be potentially more beneficial with regard to chick growth and the cost of chick-rearing. Other potential beneficial effects, like the possible benefit of coprophagy on the microbial constituents and subsequent digestion of young chicks have been referenced (Cooper, 2000). Ostrich chicks have a great preference for green what?, although Cooper (2004) suggested that lucerne not be fed to young chicks as it corresponded with elevated mortalities due to impaction. In this study, however, lucerne was indeed available to the foster chicks. Since feeding behaviour is learnt from observing adults in the wild, the presence of the foster parents may enhance feeding behaviour (Aganga *et al.*, 2003). Although it was not quantified, it was observed that the human imprinted chicks exhibited a greater degree of feather pecking, pecking at the air and general pecking behaviour that was alleviated when the group was split into three separate pens, but which may have contributed to inhibited growth (Lambert *et al.*, 1995). The human imprinted chicks may also have experienced stress subsequent to the perceived abandonment by the imprinting subject at 30 days post hatch. This stress may have inhibited the growth of the imprinted chicks (Laugero & Moberg, 2000), but it was not reflected in their survival from 4 to 12 weeks. When late chick survival (from 13 to 24 weeks) was considered, chicks reared by foster parents had an improved survival relative to the imprinted chicks (Table 6.1). Although the results are not directly comparable, it is notable that Janse van Vuuren (2008) reported that chicks with foster parents survived better than those subjected to conventional rearing in her study.

Table 6.1 The effect of rearing by adult foster parents and human imprinting of ostrich chicks on 0 to 24 week survival (0-24WKS), 0 to 12 week survival (0-12WKS), 0 to 3 week survival (0-3WKS), 4 to 12 week survival (4-12WKS), 13 to 24 week survival (13-24WKS), 4 week chick weight, 9 week chick weight, 18 week chick weight and 22 week chick weight with their respective p-values and Chi-square (χ^2) values for survival. Survival is expressed as proportions, while live weights were measured in kg.

Trait	Foster parents	Imprinted	χ^2 or F*	df*	P value
Survival					
0-3WKS	0.89	0.90	0.00	1	ns
0-12WKS	0.77	0.74	0.24	1	ns
0-24WKS	0.70	0.52	6.71	1	< 0.05
4-12WKS	0.83	0.86	0.06	1	ns
13-24WKS	0.91	0.61	9.38	1	< 0.05
Chick weight					
4 Weeks	2.1 \pm 0.07	2.3 \pm 0.08	2.6	1,108	ns
9 Weeks	12.8 \pm 0.4	8.2 \pm 0.4	70.7	1,106	< 0.001
18 Weeks	37.1 \pm 0.8	19.9 \pm 0.8	221.8	1,109	< 0.001
22 Weeks	46.2 \pm 1.1	28.6 \pm 1.2	119.9	1,109	< 0.001

*Denotes the appropriate χ^2 - or F-values, as well as the degrees of freedom (df) for the 2 x 2 contingency table for the χ^2 analysis, as well as for the treatments and the residual in the one-way ANOVA

Chicks in the care of breeder pair 21 exhibited reduced survival and growth compared to the other two breeder pairs (Table 5.2). Cumulative survival to 24 weeks post-hatch was 0.54 for those chicks raised by breeder pair 21, significantly lower than that of the breeder pairs 23 and 29 (Table 6.2; 0.90 and 0.71 respectively). Breeder pair 23, on the other hand had the highest chick survival to 24 weeks of age as well as the heaviest chick weights recorded during all weighing sessions (Table 6.2). It is notable that breeder pair 21 had the youngest male (9 years), while breeder pair 23 had the oldest male and female. The performance of the respective pairs may thus reflect the age and parental experience of the adult ostriches. The appropriate behavioural components should be investigated further.

Table 6.2 The effect of rearing of ostrich chicks by different adult foster parents on 0 to 24 week survival (0-24WKS), 0 to 12 week survival (0-12WKS), 0 to 3 week survival (0-3WKS), 4 to 12 week survival (4-12WKS), 13 to 24 week survival (13-24WKS), 4 week chick weight, 9 week chick weight and 22 week chick weight with their respective p-values and Chi-square (Chi²) values for survival. Survival is expressed as proportions, while live weights were measured in kg.

Trait	BP21	BP23	BP29	Chi ² or F*	df*	P value
Survival						
0-3WKS	0.87	0.95	0.90	0.77	2	ns
0-12WKS	0.58	0.90	0.95	7.06	2	<0.05
0-24WKS	0.54	0.90	0.71	6.23	2	<0.05
4-12WKS	0.67	0.95	0.93	7.10	2	<0.05
13-24WKS	0.93	1.00	0.85	0.54	2	ns
Chick weight						
4 Weeks	1.67 ± 0.14	2.35 ± 0.13	2.16 ± 0.11	6.74	2, 54	<0.05
9 Weeks	10.27 ± 0.71	13.67 ± 0.65	13.54 ± 0.54	8.11	2, 54	< 0.001
22 Weeks	35.8 ± 1.73	38.43 ± 1.54	36.62 ± 1.34	0.72	2, 54	ns

*Denotes the appropriate Chi²- or F-values, as well as the degrees of freedom (df) for the 2 x 2 contingency table for the Chi² analysis, as well as for the treatments and the residual in the one-way ANOVA

In Experiment 2, chicks raised with deliberate and regular human care exhibited better early chick survival to 3 weeks of age compared with the conventional rearing treatment ($P < 0.05$; Table 6.3). This resembles findings in young poultry where antibody production, disease resistance and mortality were all constructively affected by regular handling (Jones & Waddington, 1992; 1993; Barnett *et al.*, 1994; Hemsworth *et al.*, 1994). After 4 weeks of age, chick survival was independent of treatment. It is worth noting that both groups of chicks were treated similarly from 4 weeks post hatch, being maintained on outdoor paddocks with *ad libitum* balanced rations available. These results suggest that imprinting, regular handling and the corresponding monitoring of conditions, stressors, and possible other impediments may have contributed towards the higher early survival of imprinted chicks. The degree to which the chicks imprinted on the human subject, however, needs to be deliberated as some chicks exhibited a greater tendency to approach, follow and remain in generally close proximity with the human subject than others. The ability of chicks to distinguish between individual people and whether habituation to one individual may extend to another should also be further deliberated (Jones, 1994; Rushen *et al.*, 1999). The human primarily involved in the regular handling was absent after 4 weeks post hatch after which survival was no

longer affected. Birds do appear to be highly sensitive to visual stimulus characteristics of people in their environment and apparently utilize these characteristics to discriminate between humans (Rushen *et al.*, 1999). It is unknown whether stimulus generalization; defined as a tendency for stimuli similar to the original stimulus in a learning situation to produce the response originally acquired, occurs in ostriches (Reber, 1988; McLennan & Horn, 1991; Barnett *et al.*, 1993).

Table 6.3 The effect of conventional handling and human imprinting of ostrich chicks on mean 0 to 3 week survival (0-3WKS), 4 to 12 week survival (4-12WKS) and 4 week chick weight with their respective P-values and Chi-square (χ^2) values for survival. Survival is expressed as proportions, while live weights were measured in kg.

Trait	Conventional handling	Imprinting	χ^2 or F	df	P value
Survival					
0-3WKS	0.84	0.97	6.44	1	< 0.05
4-12WKS	0.69	0.73	0.14	1	ns
Chick weight					
4 Weeks	6.18 \pm 0.17	6.27 \pm 0.16	0.14	1,93	ns
9 Weeks	15.2 \pm 0.70	16.5 \pm 0.68	1.90	1,93	ns

*Denotes the appropriate χ^2 - or F-values, as well as the degrees of freedom (df) for the 2 x 2 contingency table for the χ^2 analysis, as well as for the treatments and the residual in the one-way ANOVA

Growth, as reflected by an increase in live weight, was independent of treatment group in this experiment (Table 6.3). This finding is similar to those of Reichman *et al.*, (1978) and Leonard & Fairfull (1992) who found regular handling to have no effect on the growth of young broilers and layers. Jones & Hughes (1981), however, demonstrated an improvement in growth and performance with regular handling. The effect of handling on production is evidently inconsistent, exhibiting an extensive array of influential variables (Rushen *et al.*, 1999). The precise mechanisms of this relationship in ostriches should be further investigated (Hemsworth *et al.*, 1994).

Overall, the present study indicated that chicks reared by foster parents and those imprinted onto humans with regular handling exhibited similar 4-week chick weights and chick survival to 3 months of age. The chicks reared by foster parents, however, attained substantially higher mean weights at older ages. Differences in the survival and growth of the different foster groups of chicks, also suggest an effect of parenting ability on the performance of chicks, which probably needs further research. On the other hand, human imprinting and regular handling corresponded

with an improved chick survival during the first few weeks post hatch in comparison with chicks reared according to conventional procedures in an intensive rearing facility, although chick weights were unaffected. Imprinting and early regular handling regimes, however, had no effect on survival at older ages.

Conclusion

This preliminary study suggests that ostrich chicks reared under semi-intensive conditions by foster-parents are heavier than chicks reared under intensive conditions imprinted on humans. Differences between the chick-rearing ability of the foster pairs were observed, which could have contributed to the significant differences observed for chick performance. In intensive rearing facilities, early survival of imprinted chicks is better than that of chicks reared by conventional practices. Imprinting thus affected early survival of ostrich chicks relative to conventional rearing.

These results indicate a number of potential further studies as important. Such studies need to assess how imprinting and foster parenting may be utilized to optimize chick performance, as both systems seem to be viable alternatives to conventional rearing. To achieve this, the innate components of behavioural preferences and stress susceptibility in ostrich chicks, as well as the behavioural aspects of good foster parenting and imprinting need to be investigated. Imprinting onto humans takes much time and effort and may be impractical for large batches of chicks typical of commercial farming industries. The potential of imprinting onto objects should however be considered together with diverse forms of environmental enrichment (classical music, dummies) that may be more practical with simultaneous favourable effects associated with reduced stress. Research differentiating regular handling and human imprinting and the effects thereof could also be of benefit. This information will be crucial to determine how both these obviously divergent strategies may be utilized to optimize survival, performance and welfare of ostrich chicks. Similarly, the obvious advantage of foster parenting for commercial chick production in terms of affordability needs to be elucidated further.

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Chapter 7

General conclusions and recommendations

The ostrich production industry is in need of management and breeding strategies that will improve the survival of chicks. Knowledge of non-genetic and genetic parameters affecting ostrich chick survival will assist in the development of such strategies. Studies in other species propose that alternative rearing methods that include environmental enrichment may be beneficial to the welfare, performance and survival of neonates. Little research has, however, been done in this area for ostriches. This study set out to establish a better understanding of aspects involving early chick survival in ostriches.

- A great degree of variation for survival during the first 6 months was demonstrated with a significant environmental component. The age of the hen affected chick survival to 12 weeks post hatch. The interaction effect of year and season was notable for all age specific survival traits up to 24 weeks post hatch. The gender of the chick affected survival at later ages (0 to 24 week survival, 0 to 12 week survival, 4 to 12 week survival and 13 to 24 week survival), with females surviving better than males. The duration of egg storage prior to incubation affected chick survival from 0 to 3 weeks of age.
- The additive genetic variance ratio for early chick survival were generally low ($h^2 = 0.06-0.12$), depending on the trait and statistical model applied.
- Day-old chick weight was positively related to age-specific chick survival on the environmental level. Corresponding genetic correlations were slightly higher in magnitude, but associated with comparatively large standard errors, and therefore not particularly accurate. The possibility of a favourable genetic correlation of day-old chick weight with survival was proposed.
- Ostrich chicks fostered by adult ostriches in a semi-intensive system were heavier at older ages, with an enhanced survival from 13 to 24 weeks and 0 to 24 weeks when compared to chicks raised intensively and imprinted onto a human subject. In contrast, early chick survival and chick weights did not differ between treatment groups.
- Early chick survival of those chicks exposed to regular human contact in an intensive rearing system was higher than that of chicks raised in an intensive rearing system with conventional handling. In contrast, the respective treatments did not affect chick weight at any stage during the study.

A number of recommendations can be made from the outcomes of this study. From this study, one can conclude that a great deal is yet to be established as pertaining to ostrich chick survival, which in turn can depend on complex interactions between the environment, genetics and managerial inputs. Considerable additional research is thus needed to ensure that chick survival is improved

- Year and season had a notable interactive effect on chick survival. Such effects are common in animal breeding, but of little practical consequence. However, statistical modelling should include these effects, to account for the significant portion of environmental variation they account for.
- Selection strategies for improved chick survival should be designed. Early chick survival and survival from 13 to 24 weeks post hatch could thereby be improved, and demonstrated the potential for selection gains.
- It was proposed that selection for heavier day old chick weights may improve early chick survival, but further research is required to validate this assumption.
- Causes of mortalities as well as chick deformities/abnormalities should be recorded. Studies in turkeys have demonstrated the walking ability of chicks to be highly correlated with leg and hip structure, as well as longevity and long-term survival. Further research into the genetic components of skeletal deformities as well as disease resistance and ambulation in ostriches should also be conducted.
- Egg storage may prove beneficial in enhancing survival of chicks during the first couple of weeks post hatch. Chicks from eggs stored for 1 day (eggs or chicks) or less demonstrated a reduced survival probability. Investigations into the effects of prolonged storage on early chick survival should be done.
- Care should be taken when handling ostrich chicks and attempts to reduce social stressors should be implemented. When selecting staff who will be handling ostrich chicks, one should consider the attitude, work ethic and behaviour of staff. There is potential to improve the welfare of young birds by recognizing and manipulating those human factors that may be influential. The determination of what chicks may perceive as aversive and the avoidance thereof with the provision of positive experiences may help in reducing stress and chick deaths. In this study, those chicks imprinted onto humans were notably easier to handle than those chicks raised by foster parents. This may be beneficial with general management of birds although the reproductive implications thereof should be fully determined and considered.
- The determination of an objective method to determine or assess the degree of imprinting and/or fearfulness of birds would enable better assessments of such behaviour and the possible implications thereof.

- The use of foster parents may be very useful and affordable in rearing chicks with improved survival and growth under intensive and semi-intensive commercial conditions. Although the use of adult ostriches may not be feasible in an intensive system, alternative foster parents such as rabbits may be worth considering. This however would need investigation as bio-security may be threatened in such a system. If adult ostriches are used, care should be taken in identifying suitable parents, as parenting ability will determine the success of such a system and may differ greatly between birds. Identifying those dynamics (i.e. rising time, time spent eating etc.) that are associated with better foster parents may present an interesting study cannot say this until study is done. The genetic and environmental components of good parenting together with the potential association with reproductive ability should also be investigated further.
- Observations during the course of this study suggest a large degree of variation between individuals in imprinting behaviour, and the tendency of chicks to be more comfortable with human interaction. If these inconsistent findings can be linked to genetic variation, there may be substantial scope for genetic selection for behavioural traits that will affect the performance of chicks in specific rearing systems. Anxiety and stress responses are demonstrated to have a significant genetic component while antagonistic interactions occurring between chicks may have important implications for survival and welfare of ostrich chicks.